JOURNAL OF AGRICULTURAL RESEARCH

VOL. 60 WASHINGTON, D. C., April 15, 1940 No. 8

MORPHOLOGY OF THE VEGETATIVE ORGANS OF SUGARCANE[1]

By ERNST ARTSCHWAGER[2]

Pathologist, Division of Sugar Plant Investigations, Bureau of Plant Industry, United States Department of Agriculture

INTRODUCTION

In selecting a basis for the description of cultivated sugarcane (*Saccharum*) varieties, characters of the inflorescence (*4*)[3] are ruled out, partly because in many localities numerous varieties bloom rarely, if ever, and partly because of lack of knowledge of the diagnostic value of flower characters.

Since the earliest records of sugarcane in literature (*25*), gross morphological characters have been used in describing varieties. Even Barber (*7, 8, 9, 10*), in his monumental work on sugarcane, relied mostly on characters of stem, leaf, and root. With increasingly wider knowledge of the plant, various investigators have made use, at one time or another, of more minute and microscopic features, such as number and disposition of root primordia in the root ring, arrangement of stomata, and character of stem epidermis. The arrangement of hair on buds and leaves received special attention from Jeswiet (*15*) in his Morphology of Sugarcane, a course of lectures designed originally for use by the scientific staff of the Java Botanical Garden, engaged in sugarcane studies. This work was the first of an extensive series of papers (*5, 6, 11, 16, 17, 18, 19, 20, 21, 22, 23, 24, 30*) dealing with the taxonomy of sugarcane varieties and of seedlings that originated at the Java station. While it treated of the vegetative organs of the plant in their entirety, it put greatest emphasis on the description of hair groups, thus emphasizing the importance of hair groups in the general classification scheme.

There is something very attractive about Jeswiet's method as a key for the difficult classification of sugarcanes. Smith (*31*) used it in his seedling studies at Hawaii, Fawcett (*14a*) in Argentina, and Cowgill [4] on some of the New Guinea varieties in the collection of the Division of Sugar Plant Investigations. However, except for these workers, Jeswiet's hair-group method has found few adherents, partly because the method is not practical as a ready means for the field identification of cane varieties and partly because, within a variety, seldom more than 50 percent of the hair groups are present on every bud and show a minimum amount of variation. It is, however, a

[1] Received for publication December 1, 1939.
[2] Credit is due Mrs. Eugenia Artschwager for preparation of the drawings.
[3] Italic numbers in parentheses refer to Literature Cited, p. 547.
[4] COWGILL, H. B. Unpublished data.

useful auxiliary method for the identification of varieties to be used by technically trained persons. Greater constancy, according to De Calvino (*12*) and Artschwager (*2*), is found in the character of the stem epidermis and, to a certain extent, in the structure of the leaf blade and leaf sheath (*26*).

The large collection of original importations by the Division of Sugar Plant Investigations gave the writer an opportunity to continue the extensive studies of sugarcane varieties interrupted by the untimely death of Cowgill, and to evaluate the usefulness of hair groups on material other than that used by the workers at the Java station. It is best to base identification upon the greatest possible number of characters, including those of external form, as has been done in the past. For this reason, characters such as shape, size, and color of internode; bud furrow; shape and size of buds and their hairiness; and form and size of ligule, auricles, and collar received as careful treatment as special methods, either already listed or newly tried, permitted.

As the work progressed, the need for a descriptive outline (*3*) more complete in its scope than the one recommended by the International Society of Sugar Cane Technologists (*27*), made itself felt. In the preparation of the new outline, the use of diagrammatic drawings illustrating type patterns of different characters was found helpful, making the data more uniform and more readily accessible for statistical studies. The hair-group numbers of Jeswiet have been retained, though with reservation; they often have great practical value, even though their regional designation may not always be acceptable.

MATERIALS AND METHODS

The material for study came from the United States Sugar Plant Field Station at Canal Point, Fla. All characters were studied and illustrations prepared from fresh material. For quick and easy reference, various parts of the plant, such as node, sheath base, ligule, dewlaps, auricles, and buds, were photographed on paper. The buds were always magnified six times and the photographs subsequently redrawn in order to show the hair groups on both surfaces to better advantage. The epidermis of stem, leaf, and sheath was easily stripped off after treatment with nitric acid. To obtain uniformly good results, it is best to dilute the concentrated acid slightly when treating leaves and to interrupt the heating before the acid comes to a boil. Removal of the stem epidermis necessitates the use of concentrated acid, to which a few crystals of potassium chlorate may be added. In a few varieties the stem epidermis does not strip easily, but even though some cortical tissue may remain attached it is usually possible to make the necessary observations and measurements and determine the epidermal pattern. To obtain better differentiation, it is advantageous to mount the stripped epidermis in zinc chloroiodide. The inner stem structure may be studied from unstained hand sections, though previous treatment with phloroglucin in alcohol and hydrochloric acid greatly simplifies the task. Ligules and auricles may be detached and mounted in dioxane balsam without preliminary treatment; such slides are permanent and may be filed for future reference.

MORPHOLOGY OF THE STALK OR CULM

Sugarcane is a tall, perennial, gregariously growing grass, with the culms bunched in stools or evenly scattered, sometimes provided with long creeping rhizomes.

THE INTERNODE

General Morphology

The length and thickness of the stalk is determined, morphologically speaking, by the size and number of nodes and internodes composing it. The number of these stem units varies with and within a given variety. They are longest in the middle of the stalk and for some distance remain fairly even in size. Generally, the length and thickness of the internodes decrease from the middle part of the stalk in both acropetal and basipetal directions. The internodes are shortest at the very base of the stalk, and their shape is usually obconoidal. Sometimes extremely short internodes are interpolated between normal ones; at other times, especially when the growing season has been marked by extremes in weather, a few exceptionally long internodes may be found.

The internodes assume their characteristic varietal shape before they reach maximum development. Their cross-sectional area is round, in some varieties oval, and their disposition on the stalk is alined or zigzag (staggered).

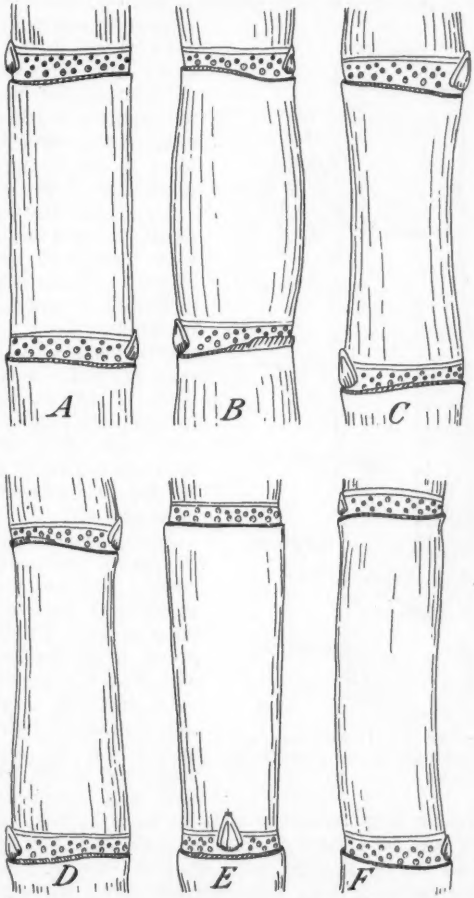


FIGURE 1.—Internode patterns: *A*, Cylindrical; *B*, tumescent; *C*, bobbin-shaped; *D*, conoidal; *E*, obconoidal; *F*, curved.

The most common forms of internodes are illustrated in figure 1. In the cylindrical internode (fig. 1, *A*) the cross section remains the same, while in the tumescent type (*B*) it is greatest near the middle, decreasing gradually in either direction. The bobbin-shaped type (*C*)

is the exact reverse of the tumescent internode, being thinnest in the middle. In the conoidal form (*D*) the diameter decreases acropetally, while in the obconoidal type (*E*) the greatest diameter is immediately below the wax band and the smallest immediately above the intercalary zone, or growth ring. The conoidal internode frequently has a bulge or shoulder directly above the growth ring on the side opposite the eye, and certain cylindrical internodes become more or less depressed on the bud side and convex on the opposite side (*F*).

Internode patterns have a certain value in classification, provided the material is from plants developed under favorable conditions. An abnormal environment is often responsible for atypical forms, which may occur on the same stalk with normal internodes.

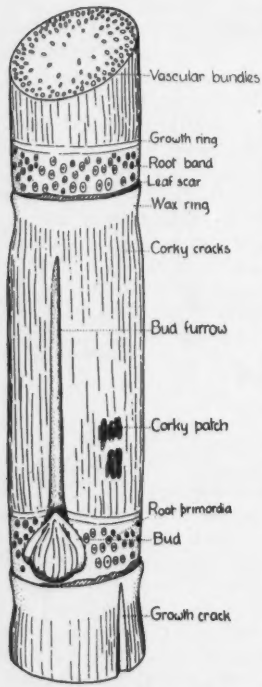


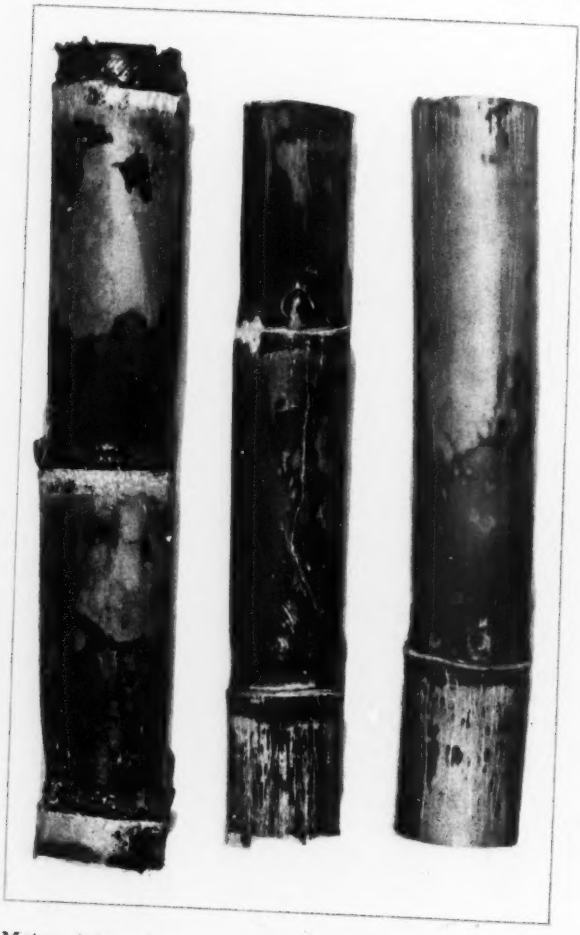
FIGURE 2.—Diagrammatic drawing of node and internode.

Color of the stalk is regarded by many experienced workers as an important character, even though Jeswiet (*15*) concluded that it would never become a basis for classification of cane varieties.

In noting the color, reference should be made to mature and exposed internodes that have not yet become faded or discolored. Color is a very obvious character; although it may vary from internode to internode, the general hue is typical for a given variety. To the inexperienced, it may seem to be a very elusive character, since environmental factors often greatly influence its expression. According to Earle (*14*) and other authors, many sugarcanes that are normally green show a pronounced reddish or brownish flush on exposure to light and air.

Striking color differences are often noted in freshly cut stem sections. In some varieties, the color of the cross section is uniform to the very center; in others, the outer zone is of a different hue, often a deep green, while the center is grayish, ivory, or whitish if the variety is pithy.

Of interest, and often a character of importance, is the bud furrow, or eye groove (fig. 2), a depression in the stalk beginning in the root band underneath the bud and extending upward. The bud furrow may be either wide or narrow, deep or shallow, long or short. It may be absent or show as a slight flattening of the stem above the bud or be limited to a shallow cavity. Sometimes the furrow is narrow and deep and extends along the entire internode, with the bud embedded in a rather deep depression. The depth and width of the furrow may be uniform throughout, though more often it tapers in the direction of the wax ring, gradually becoming narrower and shallower. The color of the bud furrow is usually like that of the rest of the internode but occasionally different.



Mature internodes of variety 28 N. G. 204, showing corky cracks and progressive stem discoloration, which give the surface the appearance of dead stalks.

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The surface of the stalk is almost always glabrous. A distinct pubescence was found in 75 Lehu (Imp.[5] 736) briefly described by Moir (*28*) in 1932, and in New Caledonia 32 (Imp. 892). Occasionally the smoothness of the surface is broken by the appearance of corky cracks or growth cracks.

Corky cracks, or ivory markings. are small longitudinal crevices in the epidermis (fig. 2). In old stalks they may appear rough and become confluent, forming corky patches. The cracks are at first the color of the internode and rather inconspicuous; later they turn whitish and may be edged with a different color. Often they are found only in older internodes, in the zone of the wax ring and immediately below, and also along the bud furrow. They may be very irregular and scattered, absent from some internodes while present in others. Occasionally their occurrence is limited to those parts of the stalk that have been much exposed to the sun; here they often unite to form gray spots or patches, which sometimes unite in a grayish ring below the wax band.

Often the surface of entire internodes becomes progressively discolored or brown (pl. 1) until the cane looks like a dead stalk. This appearance is effected by color changes in the hypodermal cells and usually takes place independently of the formation of cracks in the epidermis.

Deeper longitudinal cracks, which extend into the tissue of the internode, are the so-called growth cracks (fig. 2). These often reach into the intercalary zone but never into the adjacent internode. They may occur along with corky cracks and are generally considered a fairly reliable character.

All parts of the stalk, with the exception of the growth ring, have a coating of wax which, in the region immediately below the sheath base, forms a more or less conspicuous white band. The waxy coating may be even and thick, often dense enough to hide the color in the young internodes, or it may be thin and uniform, giving the surface a glazed appearance. In some varieties, bloom is practically absent, and then even the wax ring is inconspicuous. In some reddish or purplish canes, the upper half of the internode is densely covered with wax that gradually becomes thinner and more transparent and disappears altogether in the basal region. When the waxy coating is very heavy, it may peel off in places, imparting to the surface of old stems a peculiar striation. In internodes that are no longer protected by the sheath and sometimes also in younger internodes, the wax may become discolored. This change in appearance may affect the entire internode, or else the discolored areas may form irregular patches varying in color from dirty white to almost black. The discoloration is usually caused by the superficial growth of certain molds.

The wax deposit is always thickest and whitest below the sheath base. Usually there is a distinct division between wax ring and general bloom, but sometimes this demarcation is faint or disappears in canes where the bloom is heavy. Then the result is a gradual and complete merging of the wax of the ring with that of the general bloom. In most cases the wax ring is conspicuous and very white. Its width is subject to much variation and may be considered a varietal character. The wax ring is always narrow in young internodes but is

[5] Imp.=Importation number assigned by the Division of Sugar Plant Investigations.

usually set off more distinctly than in older internodes. In a few varieties the ring is distinctly striated (New Caledonia 92, Imp. 913). Sometimes the wax of the ring, like that of the general bloom, becomes discolored in older internodes and may peel off in patches or entirely.

The tissue of the internode consists of vascular bundles embedded in parenchyma. The bundles are rather widely spaced in the central part. Occasionally the center becomes pithy, and in certain wild forms a distinct cavity develops. The number of bundles increases centrifugally. At the periphery they lie very close together often forming a solid ring (pl. 2, *A*, *B*). All bundles are surrounded by a sclerenchymatous sheath, which is most strongly developed in the peripheral bundles. The outermost ring may be composed altogether of small bundles or of small bundles alternating with larger ones (*B*). Relative size and spacing of the bundles is not correlated with thickness of the internode.

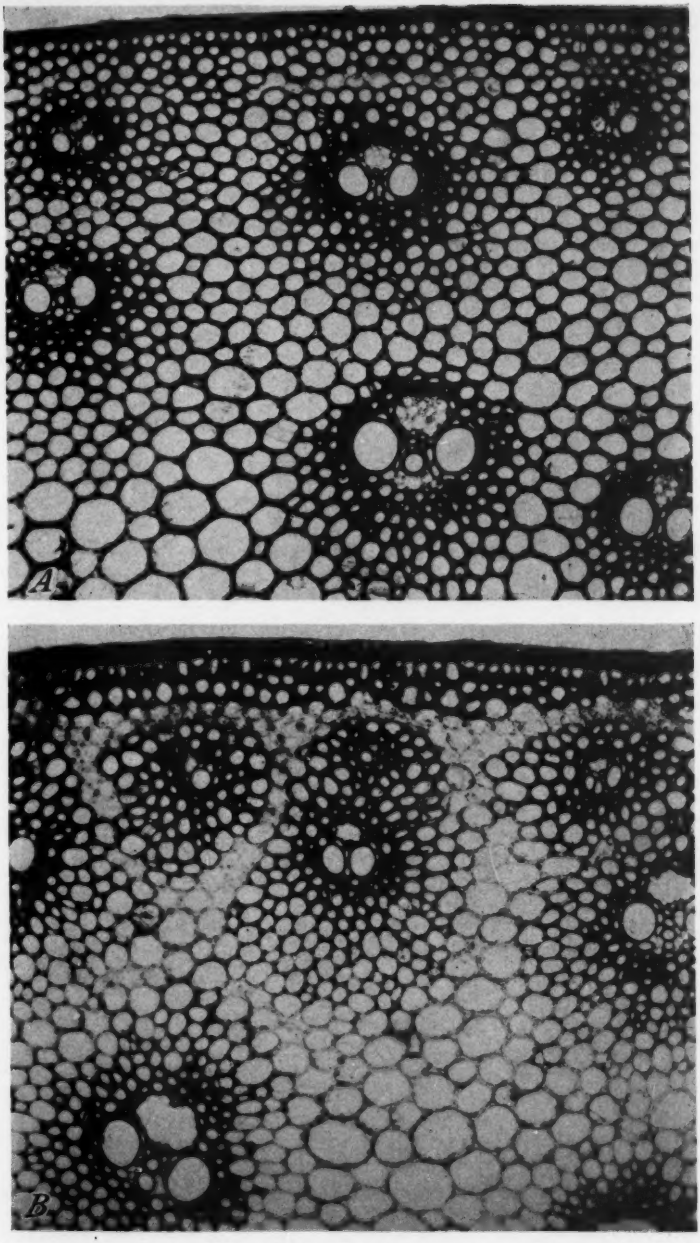
Table 1 indicates the extent of relationship between bundle density in the peripheral ring and thickness of internode. One would expect a larger number of bundles per unit area in the thin canes than in the thick-stemmed forms, yet in many of the very thin wild canes the bundles are rather widely spaced. The number of bundles in the outermost ring is often, though not always, influenced by their size. If the number is large, all peripheral bundles are likely to be small, and conversely a very small bundle number indicates that at least some of the peripheral bundles are of the large type. Although there is some variation within a variety, bundle density within the peripheral ring and relative size of these bundles constitute a valuable character.

TABLE 1.—*Relation between thickness of stem, total number of bundles, and number of bundles in peripheral ring as seen at the widest diameter of a microscopic field covered by a 16-mm. objective and a ×6 eyepiece.*

Variety	Importation No. [1]	Diameter of stem	Bundles		Variety	Importation No. [1]	Diameter of stem	Bundles	
			Total	Peripheral				Total	Peripheral
		Millimeters	*Number*	*Number*			*Millimeters*	*Number*	*Number*
Shantir Barhni	142	7	10	5	New Caledonia 31	891	36	11	4
U. S. Imp. 229	229	11	7	6	New Caledonia 32	892	39	8	3
Tabongo	578	11	10	4	New Caledonia 33	893	36	10	5
Hemja	234	22	10	6	New Caledonia 40	897	38	10	5
Nagori	235	17	9	5	New Caledonia 42	898	34	6	4
Manjav	95	24	14	6	New Caledonia 50	902	33	9	4
Kinar	6	21	7	3	New Caledonia 51	894	43	9	4
Merthi	7	21	11	3	New Caledonia 53	895	31	12	5
Fiji 3	862	15	14	5	New Caledonia 59	899	33	10	5
Hawaiian Original 6	825	35	14	6	New Caledonia 64	901	24	12	6
Hawaiian Original 26	828	29	13	6	New Caledonia 74	903	35	9	4
Hawaiian Original 38	832	34	12	6	New Caledonia 76	904	33	9	5
Hawaiian Original 43	836	34	14	5	New Caledonia 78	905	38	10	4
New Caledonia 20	885	28	13	9	New Caledonia 80	906	29	9	4
New Caledonia 21	886	34	7	3	New Caledonia 81	908	40	10	5
New Caledonia 25	888	38	10	5	New Caledonia 83	910	29	12	5
New Caledonia 30	890	25	11	8	New Caledonia 92	913	29	12	5
					New Caledonia 93	914	29	7	4
					New Caledonia 99	917	38	11	6

[1] Assigned by the Division of Sugar Plant Investigations.

The peripheral ring is separated from the epidermis by a very narrow cortex, not more than four cells wide. The cells of the two rows next to the epidermis are small, usually thick-walled, and in



A, Partial stem section of U. S. 859. Peripheral bundles well separated; peripheral cells and surrounding parenchyma thick-walled and heavily lignified. *B*, Partial stem section of P. O. J. 2714. The sheaths of the outer row of bundles are very large and confluent. Both × 300.

mature stalks heavily lignified. Adjacent to this layer are one or two rows of thin-walled parenchyma cells with chloroplasts. The walls of these cells remain cellulose even in old and mature stalks.

The central stem bundles have a bundle sheath that is relatively wider at the phloem and xylem poles than at the sides, where it is usually restricted to one or two layers. The width of the sheath at the two sides is more or less constant, but there may be a considerable difference in the thickness of the cell walls and in the degree of lignification. The parenchyma cells which constitute the filler between the bundles, are usually thin-walled; but in some varieties, and especially in wild canes, they may become fairly thick-walled and even lignified. Commonly there are no color differences within the tissue of the vascular bundles, but Jeswiet (*15*) reports for some varieties sheaths of a characteristic dark-brown color.

Structure of Stem Epidermis

Types of Cells

The essential structure of the stem epidermis has been described in an earlier publication (*2*). It is in agreement with the type of structure that obtains in grasses in general. The epidermis consists of a single layer of different kinds of cells, of which each kind may vary as to size and number but, on the whole, forms a uniform pattern characteristic of the variety. There are three kinds of cells: Long cells, cork cells, and silica cells. Frequently a few scattered stomata are found, and there is a definite pubescence present in New Caledonia 32 and in 75 Lehu.

The long cells form four-sided prisms with undulating, strongly silicified walls. In some varieties many of these cells are completely filled with crystal sand (a form of calcium oxalate crystals). There is considerable variation in the length of these cells and in the slope of their end walls; the latter are commonly straight, though often pointed. The variation in width of the long cells appears very slight in many cultivated varieties because of the presence of intermediate forms, but it is quite apparent when varieties with very wide and very narrow cells are compared. There is no correlation between cell width and stem thickness; in many thin-stemmed wild canes the epidermal cells are very wide, while in some thick-stemmed noble varieties these cells are relatively narrow.

Exceedingly narrow epidermal cells were found in Fiji 2 and Fiji 3, but here again the thinner-stemmed variety had wider cells than the thicker-stemmed one. Tabongo (*Saccharum spontaneum*), with a stem only 11 mm. across, had as wide a cell as New Caledonia 51, which has a stem four times as thick (table 2).

The cork cells are relatively thin-walled and suberized. They occur in a wide variety of forms: Squarish, rhomboid, reniform, elongate-rectangular, and long- or short-pointed. Often a single pattern prevails, but sometimes different patterns are seen in a single microscopic field. Cork cells often appear singly, separated from one another by long cells; frequently they are grouped in twos and threes. Most often, however, they are adjacent to a silica cell, forming a typical short group so characteristic of the grass epidermis.

TABLE 2.—*Relation between thickness of stem and width of epidermal cells*

Variety	Importation No. [1]	Diameter of stem	Width of epidermal cells	Variety	Importation No. [1]	Diameter of stem	Width of epidermal cells
		Millimeters	*Microns*			*Millimeters*	*Microns*
Shantir Barhni	142	7	10.7	Hawaiian Original 24	827	38	11.0
U. S., Imp. 229	229	11	11.8	Hawaiian Original 38	832	34	8.4
Tabongo	578	11	13.7	New Caledonia 20	885	28	10.3
Hemja	234	22	11.0	New Caledonia 25	888	38	9.0
Nagori	235	17	11.0	New Caledonia 30	890	25	10.7
Manjav	95	24	11.4	New Caledonia 31	891	37	13.2
Kinar	6	21	12.2	New Caledonia 32	892	39	12.2
Merthi	7	21	12.7	New Caledonia 33	893	36	11.0
Fiji 2	861	22	7.0	New Caledonia 40	897	38	9.4
Fiji 3	862	16	9.2	New Caledonia 51	894	43	14.3
Hawaiian Original 6	825	35	9.7				

[1] Assigned by the Division of Sugar Plant Investigations.

The silica cells are much more uniform than the cork cells. They are usually biscuit-shaped, with a constricted center and overhanging margins, and with the long diameter parallel to the long axis of the stem. Silica cells rarely occur alone between long cells but are rather associated with cork cells. In some varieties they are almost altogether absent, and in many they are lacking from about 50 percent of the short groups.

Stomata are comparatively few or entirely wanting. There is a certain degree of regional distribution. Frequently stomata appear in broken rows wherever they are relatively numerous; when scarce, their location is quite erratic. In one variety with a vertically striped wax ring, stomata were found almost exclusively in the areas where there was no wax.

The following criteria proved to be of value in classifying varieties on the basis of epidermal patterns of the stems:

(A) Primary characters.
  (1) Absence of silica cells.
  (2) Prevalence of pointed cork cells.
  (3) Occurrence of cork and silica cells in multiple pairs.
  (4) Prevalence of very long rectangular cork cells.

(B) Secondary characters.
  (1) Relative abundance of stomata.
  (2) Width of long cells.
  (3) Average number of short-cell groups in a microscopic field.

EPIDERMAL PATTERNS

Type 1.—Cork and silica cells in single pairs alternating with long cells. The latter have usually straight-running, undulate vertical walls and straight or somewhat sloping end walls (pl. 3, *A*).

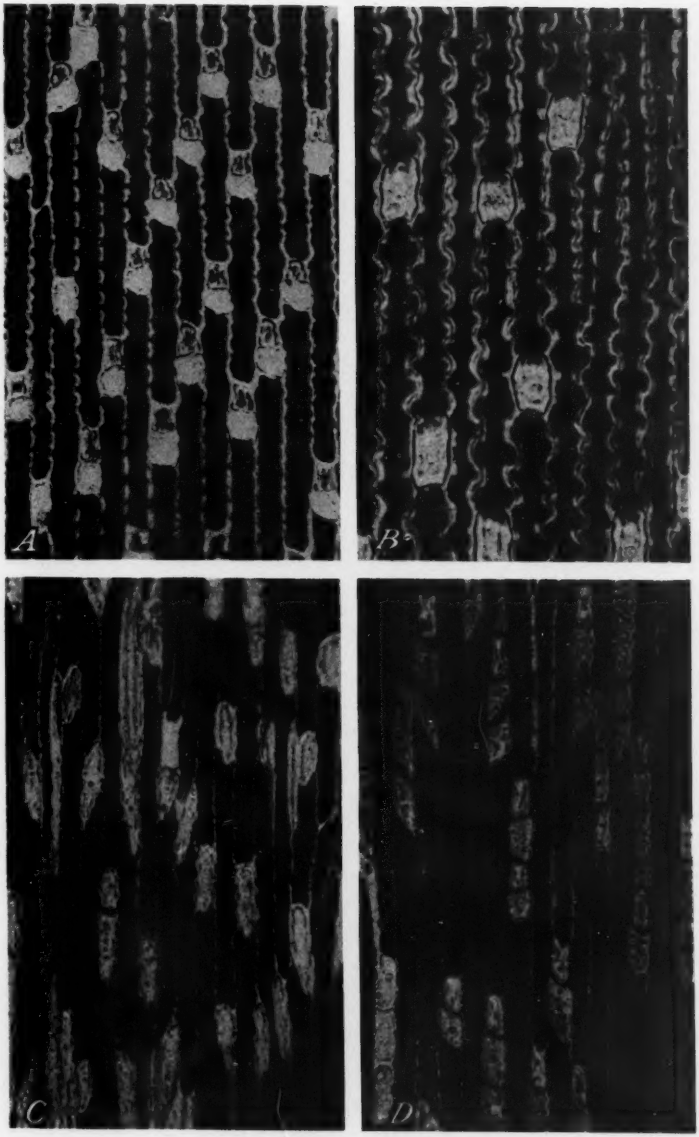
Type 2.—Silica cells wanting or very scarce. Cork cells solitary or in groups; squarish, rhomboid, or, in some varieties, greatly pointed and interspersed with the narrow elongate-rectangular type (pl. 3, *B*).

Type 3.—About 50 percent of the short-cell groups lack silica cells; the shape and distribution of the different cell forms show much variation otherwise.

Type 4.—Practically all cork cells are pointed. The vertical walls of the long cells are often curved and their end walls pointed. There is much difference in the width of the long cells. The number of short-cell groups lacking silica cells may show considerable variation. If this number is approximately 50 percent, the pattern formula would be expressed as 4+3 (pl. 3, *C*).

Type 5.—All cells are rather narrow and there is a predominance of the elongate-rectangular type of cork cell, occurring singly or in short connected rows.

Type 6.—The short-cell groups are very numerous and always occur in multiple pairs (pl. 3, *D*). The cork cells are usually somewhat elongate, squarish, or rhomboid.



Surface view of stem epidermis illustrating (*A*) Pattern 1, (*B*) pattern 2, (*C*) pattern 4, (*D*) pattern 6. All × 500.

The different epidermal patterns are not equally abundant. Table 3 shows their frequency distribution in a random collection of 100 varieties.

Types 1, 2, and 4 are the most frequent. If only single characters and not combination types are used, the numbers listed under 2+4 and 3+4 would have to be redistributed. They could all be put in type 4, raising the frequency distribution in this group to 35; or, if we consider type 2 more fundamental than type 4, the nine varieties listed under 2+4 could be added to type 2, raising the frequency distribution of that group to 26. However, combination groupings are more descriptive and characterize the variety better. They are best used when characters are not strongly developed; this applies especially to pattern 4. Long- and short-pointed cork cells, which characterize this pattern, may be relatively scarce or abundant. If their number is small, it is best to designate the epidermis where they occur by a combination formula.

TABLE 3.—*Frequency distribution of varieties according to epidermal pattern*

Item	Pure type						Combination type	
Pattern type	1	2	3	4	5	6	2+4	3+4
Frequency	20	17	14	16	5	9	9	10

The relative value of the epidermal pattern in classification may be debatable or even questionable if applied to a rather homogeneous natural group. It failed to give satisfactory results for Panje (*29*) in his studies of *Saccharum spontaneum*. But even here, Burma (*S. spontaneum*) stood out among all other forms by the fact that practically no silica cells occurred in its epidermis. The epidermal pattern may be used only as an auxiliary method in a general classification scheme, but sometimes it alone suffices to make a doubtful grouping positive, especially if the forms in question have entirely contrasting epidermal patterns.

THE NODE

The node is usually somewhat thinner than the internode and exhibits the following regions: Node proper, a zone of anastomosing and horizontally running leaf-trace bundles (*1*), limited above by the sheath scar; and root band, which contains the bud and several rows of root primordia. The growth ring, or intercalary zone, connects node with internode.

GROWTH RING

The growth ring is located directly above the root band and stands off from the latter and the internode above as a rather narrow band. It differs somewhat in color from the rest of the stem and lacks the wax deposit found on other organs of the plant.

The growth ring commonly runs horizontally or turns slightly upward above the bud or occasionally is very much arched in this region. Usually it is flush with the adjacent internodal tissue but may be somewhat depressed, most noticeably so in young stems. In older stems, it frequently bulges as a narrow ridge on the bud side or around the entire circumference (pl. 4, *D*).

In some varieties the growth ring is narrow and inconspicuous; in others, quite broad (pl. 4, *B*), a characteristic of many wild canes. Sometimes it is unequal in width all around or wider on one side than on the other; this occurs where the stalk has bent or straightened itself through the activity of the cells of the intercalary meristem.

The color of the growth ring varies in inmature and grown stalks. It is at first somewhat different from the internode; on maturing, it may retain this difference or become concolorous with the internode.

Root Band

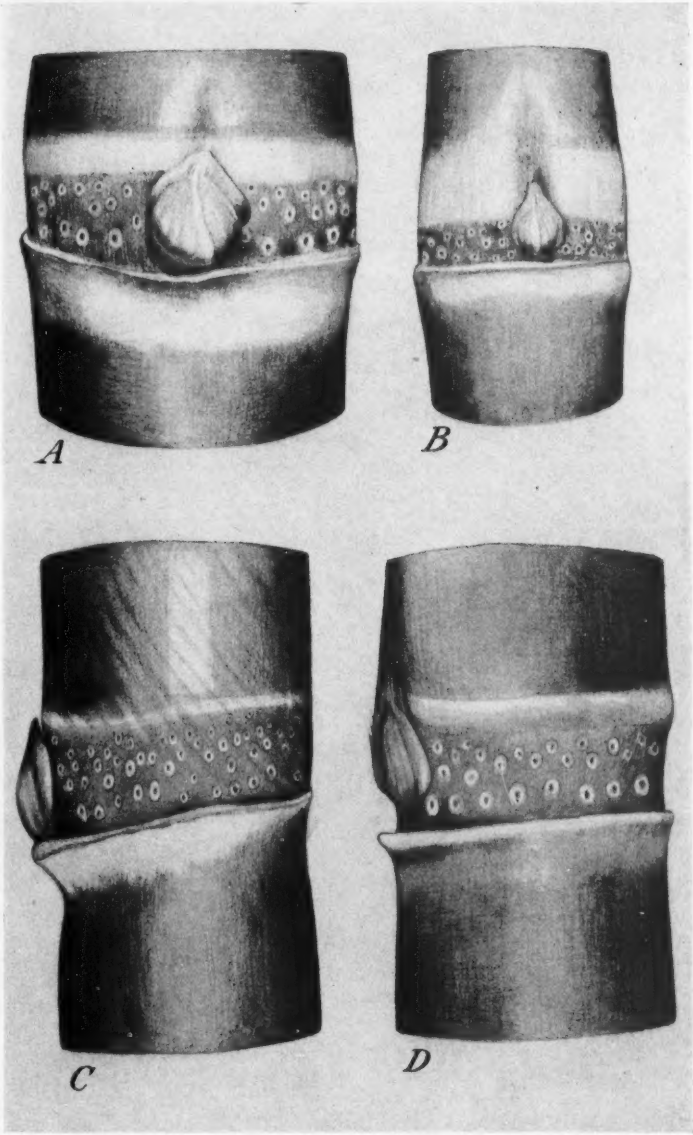
The root band is limited by the sheath scar below and growth ring above and contains, besides the bud, several rows of root primordia. It is almost colorless in young nodes but eventually becomes more or less concolorous with the rest of the stem. It varies in height, being usually taller on the side of the bud than on the opposite side. Sometimes it is slightly or prominently curved on the bud side. The root ring has a distinct coating of wax, which at times may be very heavy; this waxy coating often bears an imprint of the veins of the adpressed leaf sheath. Hairs on the root band were observed in New Caledonia 32 and 75 Lehu, two selections that are prominently hairy all over the stem.

The shape of the root ring is often characteristic of the variety. The most common form is cylindrical. Sometimes the ring is cylindrical on the bud side and obconoidal on the opposite side. Often obconoidal internodes have a conoidal root band, this shape being equally pronounced in tall and narrow root bands. In stems with prominent and swollen growth rings, the root band is frequently constricted (pl. 4, *D*) or depressed only on the side opposite the bud. Tumescent root rings are not uncommon; the swelling may be regional, often restricted to the bud zone. Obconoidal root bands are often associated with conoidal and sometimes with bobbin-shaped internodes.

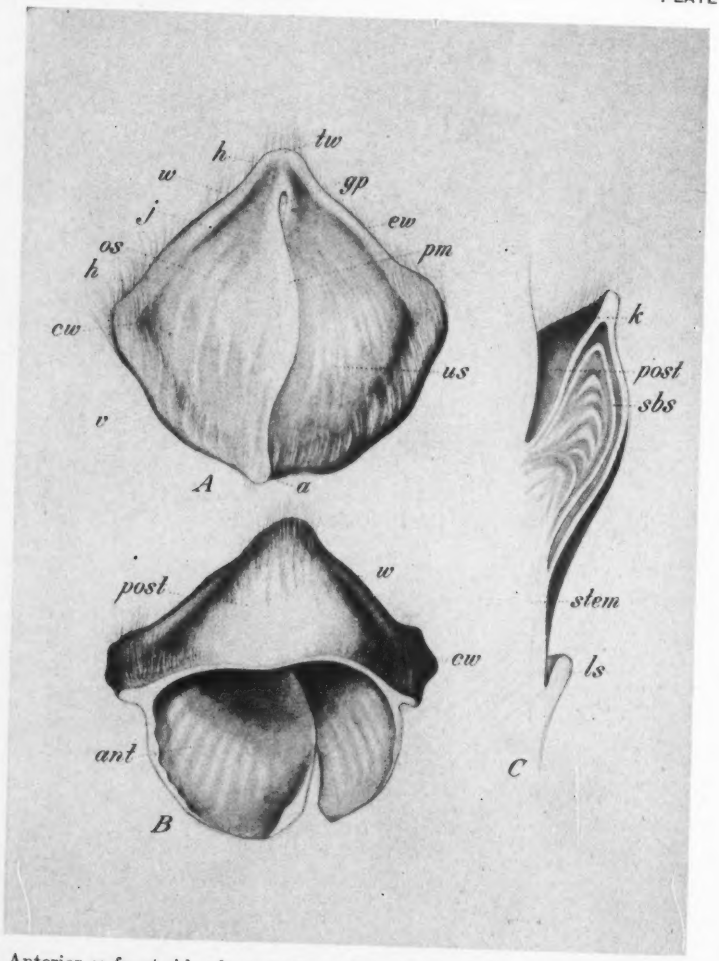
The root primordia are the initials of secondary roots. They occur in one or in several regularly or irregularly arranged rows. In wild canes, only one or two rows are found, even when the root band is rather tall. The number of rows of root primordia in a root band is usually greater on the side with the bud, although this region is not always broader than the side opposite the bud. In some narrow root bands with numerous rows of root primordia, the upper row may continue above the eye. Sometimes the root primordia in the different rows are disposed vertically, one above the other, but more often they are arranged in an oblique ascending series. Frequently the arrangement is irregular (pl. 4, *C*), a condition more common in root bands where the root primordia are numerous than in bands where they are not crowded.

The root primordia in a row are generally uniform in size; the top row in the root band contains the smallest primordia and the bottom row the largest (pl. 4, *A*). In a given stalk, the basal nodes have fewer rows of root primordia than the nodes nearer the middle. There is no further decrease in the number of rows toward the top.

Each root primordium has a dark center and a light-colored margin or "halo." The dark center constitutes the root cap, which is usually intensely colored. In young nodes the primordia are commonly visible as dark points in translucent surroundings. The colored center



Types of nodal region: *A*, Growth ring medium wide; root band with large, widely spaced root primordia. New Caledonia 24. *B*, Growth ring very wide; root band very narrow with small, more or less crowded root primordia. 28 N. G. 49. *C*, Growth ring very narrow; root band broad with many irregular rows of crowded root primordia; sheath scar protruding and spreading under bud. Haak Kwat Che. *D*, Growth ring medium wide and swollen; root band wide with large, widely spaced root primordia. Bud is inserted above sheath scar and projects above growth ring. Hawaiian Original 39. All × 1½.



A, Anterior or front side of prophyllum; *B*, posterior or back side of prophyllum; *C*, view of bud cut longitudinally to show structure and attachment of prophyllum. In its entirety, the prophyllum forms a hood, with the front side the larger and composed of two overlapping halves, and with the posterior side entire. All × 7. *a*, Appendage of overlying half of anterior side; *ant*, anterior side of prophyllum; *cw*, corner of wing; *ew*, edge of wing; *gp*, germ pore; *h*, hairs; *j*, juncture of wing with anterior side; *k*, keel; *ls*, leaf sheath scar; *os*, overlying half of anterior side; *pm*, parenchymatous margin of overlying half of anterior side; *post*, posterior side of prophyllum; *sbs*, second bud scale; *tw*, tip of wing; *us*, underlying half of anterior side; *v*, veins; *w*, wing.

is slightly raised and sometimes protrudes wartlike, especially in older nodes. The surrounding border is always lighter-colored than the center; its shape is round, occasionally oval. Its width varies from narrow to broad. The border, or halo, is usually flush with the surrounding tissue but is occasionally depressed, especially in young material. The root primordia remain dormant in many varieties, but in some they show a tendency to sprout and produce air roots while the stalks are still actively growing in the field.

THE BUD

General Morphology

The buds, or eyes, of sugarcane are small conchate organs inserted in the tissue of the node just above the leaf scar. The visible part of the bud is the outermost bud scale, or prophyllum, composed of the sides and the wing. The prophyllum in its entirety forms a kind of asymmetrical hood (pl. 5, *A*, *B*, *C*) with the anterior or front side composed of two overlapping halves and with the relatively short posterior side entire and basally limited by a curved line at which it attaches to the tissue of the node.

The edge of the overlapping half of the anterior side is drawn out to form a membranous margin, which extends from the germ pore downward and frequently terminates in an appendage. As the bud matures, the tissue of the membranous border becomes dry and the basal appendage darkens and shrivels. In some varieties the membranous border is uniformly narrow throughout; and, if the degree of overlap between the two halves of the anterior side is small, the two margins occasionally alternate; i.e., the underlying margin becomes the overlying one for a short distance. Usually the membranous border is narrow only in the region of the germ pore, becoming gradually or abruptly broader at the base. The basal appendage projects in most varieties somewhat below the level of the bud insertion, but in some it is found rather high (fig. 3, *A*). It varies greatly in general appearance and prominence, even on the same stalk. Occasionally smaller accessory appendages are present on either the upper or the underlying margin of the scale. Unusual forms of such accessory lobes are described and illustrated by Jeswiet (*23*) for Black Cheribon and certain other varieties. In addition to the basal appendage, we find in certain varieties lateral outgrowths at any point of the membranous border (fig. 3, *B*). Of these, the oblique terminal outgrowth (fig. 5, *A*, *B*), which often covers the germ pore, is especially conspicuous.

The wing of the prophyllum is formed by the two flattened and attenuated keels (pl. 5, *C*). It varies in size and prominence, and its shape influences the shape of the bud. The boundary line between wing and sides, the so-called juncture, is not always clearly marked; but usually a more or less distinct groove, which is especially prominent in the basal corners, is present. In most buds the wing originates below the middle of the anterior side of the prophyllum (fig. 3, *A*); this is generally true of long-triangular and ovate buds. In other types the point of insertion may be intermediate or relatively high (fig. 3, *B*). The latter type of insertion gives rise to the more unusual bud forms.

Relative size of wings varies greatly in different varieties. The wing may be uniformly wide over its entire length, or it may be wider or narrower at the base than at the apex; sometimes it is very irregularly lobed. Often the wing is very broad at the base and, in addition, is more or less prominently auriculate. However, well-developed au-

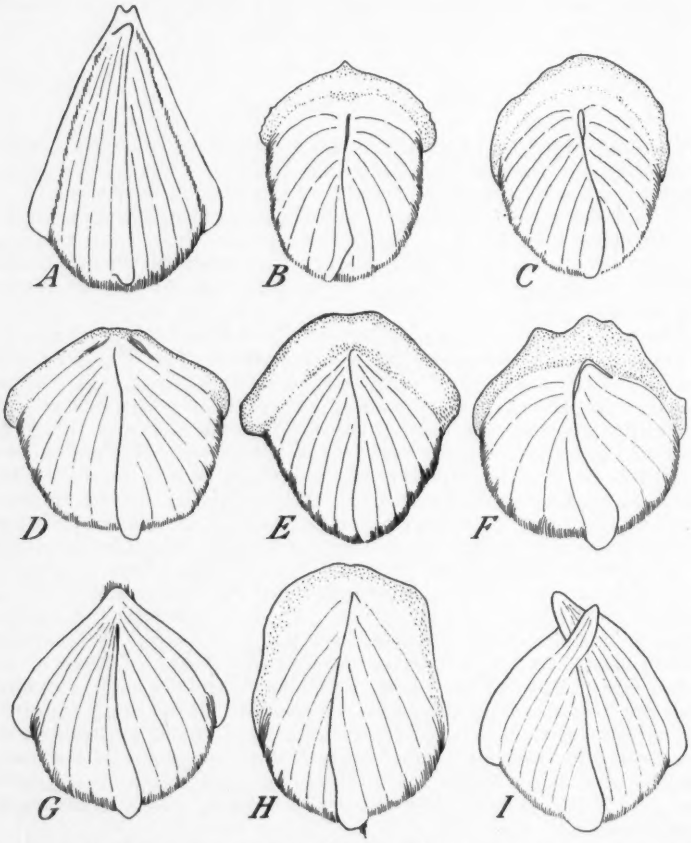


FIGURE 3.—Bud patterns: *A*, Triangular-pointed; *B*, oval; *C*, obovate; *D*, pentagonal; *E*, rhomboid; *F*, round; *G*, ovate; *H*, rectangular; *I*, beaked.

ricles are not restricted to basally wide wings. At times prominent auricles are found on only one side of the wing, being inconspicuous or absent on the other side. This is a phenomenon quite in keeping with the general tendency toward asymmetry in the development of the different organs of sugarcane.

The surface of the wing is usually flat; but in young buds, sometimes also in older ones, it is goffered or crimped. The edges of the wing also exhibit typical form patterns. Frequently the entire wing

is coarsely notched or emarginate; sometimes only the base is notched while the rest of the wing is entire. Quite often, however, the entire edge of the wing is smooth.

The apex of the bud has a characteristic shape, which is a part of the general bud pattern. The apex may be broadly triangular or crescentiform, occasionally with a flat or depressed truncate tip. Such forms are usually found in broad buds and in those where the wing is inserted high above the middle of the prophyllum. Very common are forms with a round- or sharp-pointed apex. If the tip of the prophyllum in either of these forms is prominently developed, the result is the beaked or rostrate type (fig. 3, *I*).

Usually the margin of the apex is like that of the wing, but sometimes it is quite different. For example, a prophyllum with otherwise smooth wings may have a tip that is deeply furcate, finely notched, or coarsely emarginate. In the broad crescent-shaped apex of certain buds there may be a single sharp projection, giving to the bud a mucronate appearance.

The anterior side of the prophyllum shows typical venation, which may be prominent or obscure. Sometimes the veins appear more conspicuous because of their contrasting coloration, as found in certain varieties. Usually the veins run almost parallel, converging in a gradual curve from base to apex. In round, and sometimes also in broad squarish buds, the veins approach the apex radially. There are, of course, many intermediate types.

The region where the two overlapping halves of the anterior side of the prophyllum unite is the location of the germ pore, a place where the growing shoot pushes through the protecting bud scales. Sometimes this place is marked by an irregular cleft (fig. 3, *F*); and sometimes it is covered over by the apical appendage of the membranous margin (fig. 3, *A*). In long buds, the location of the germ pore is near the tip; whereas, in round buds, in which the arrangement of the veins approaches the radial, the germ pore is central.

Much variation in both size and general appearance of buds is found not only in those of different varieties but frequently in those coming from the same stalk. However, if normally developed stalks are selected, varietal differences overshadow individual variation. Only fully developed buds should be chosen for comparison, preferably those coming from underneath fully developed leaves that are still attached to the plant. Depending on the variety, buds may be large or small, long or short, flat or plump. Young buds are always rather flat; later they become arched and attain a certain degree of fullness that is more pronounced in one variety than in another.

The tip of the bud may extend some distance above the growth ring (pl. 4, *D*), especially in large and elongated buds. In small, round buds and often in other types where the wing is inserted very high, the tip may reach to the intercalary zone (pl. 4, A) or stop short of it.

Sugarcane buds exhibit a most diverse variety of morphological forms; these have been loosely grouped under eight types. In selecting these patterns, little attention was paid to the appearance of the wings, although certain wing types are fundamentally associated with special bud forms. These bud patterns are illustrated in figure 3. The most common form is the ovate bud, which may be either elongate

(fig. 3, *A*) or broad. Quite common is the pentagonal form (*D*), usually associated with a high-inserted, rather broad wing. The oval (*B*) and obovate (*C*) types are less frequent. The ovate type has usually a high-implanted wing; in the obovate type, the position of wing insertion is less definite. Typical round buds (*F*) are not common; a related form, the rhomboid (*E*), is only occasionally found. At times the shape of the wing completely changes an otherwise typical bud pattern, as in figure 3, *H*, in which an abnormally developed wing changes an otherwise typically ovate bud into an aberrant rectangular form. Crossed beaked tips (*I*)[6] produce a very striking effect and easily characterize a variety, provided this character is constant and not limited to a few buds on a stalk.

The color of mature buds that are still protected by leaf sheaths approximates that of the stalk. Contrasting colors are apt to occur in young buds; aging buds, regardless of previous coloration, are usually gray-brown. Red buds, and often green buds, are yellow when young, and an indistinct brown when aged. Often young buds are pale green with a contrasting reddish tint in tip and wing.

The buds are placed alternately on the stem, each node bearing a single bud. Buds are occasionally absent or underdeveloped in the basal part of the stalk, and occasionally a node is found bearing two buds in juxtaposition. Jeswiet (*15*) reports the occurrence of doubling due to splitting of the normal bud, and also the development of adventitious buds, which are either axillary or found on any part of the internode.

The buds are commonly inserted directly above the leaf scar, but in many wild canes and in some of their hybrids they occur some distance above, as high as the middle of the root ring. Occasionally, the buds appear to be inserted some distance below the leaf scar. Such canes usually have sagging leaf bases and protruding sheath scars.

Much variation is found in regard to the position of the bud on the stalk. Sometimes buds that are inserted rather low are located in a cavity and then seem very much appressed; this condition is often found in canes with a deep and well-developed bud furrow. Young buds are usually appressed, and in certain varieties even mature buds retain this tendency. When buds mature they frequently protrude, pointing away from the stalk at an oblique angle. Buds with a varietal tendency to protrude are associated with cane varieties in which the internodes are conoidal.

Pubescence of Prophyllum

The buds of sugarcane, like those of other grasses, are covered with hair. In some varieties the buds are completely covered; in others the hairs are chiefly on the wings. Many cultivated forms are only moderately hairy, and some are almost entirely glabrous.

The hairs on the prophyllum are either long, white, often curved, and strongly appressed, or very short and of a brownish or blackish color. The brown hairs, which Jeswiet (*15*) regards as the primitive form, are often covered up by long white hairs.

The hairs are commonly concentrated in groups that are similar or identical in corresponding regions of the two overlapping halves of the

[6] Redrawn from Jeswiet (*15*).

prophyllum. Some of the groups are again duplicated on the posterior side; i. e., certain groups are actually present in multiples of four, although Jeswiet (*15*) uses different numbers for them.

Before entering into any discussion of their relative merit, the author will give a condensed form of Jeswiet's (*15*) original descriptions. In the following list, the groups are arranged not in numerical order but rather according to their distribution on sides, wing, and juncture of the prophyllum. Diagrammatic sketches, showing the regional distribution of these hair groups are given in figure 4.

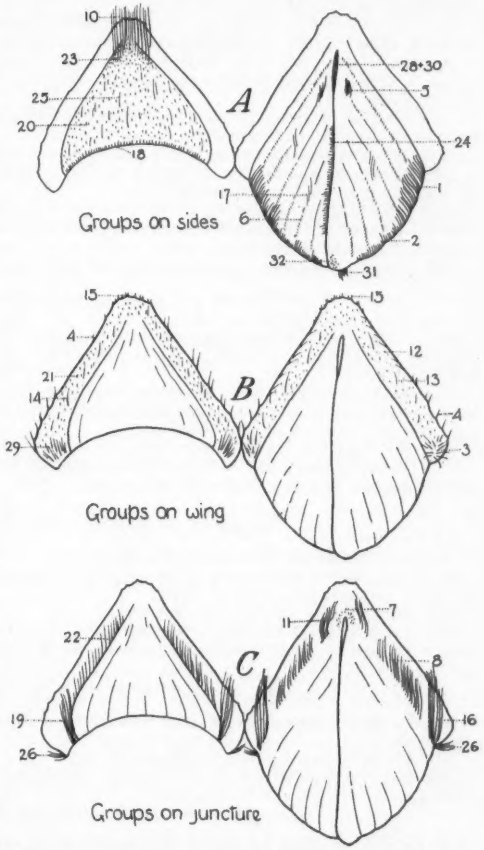


FIGURE 4.—Diagrammatic drawing of prophyllum replicated three times, showing location of hair groups (*A*) on sides, (*B*) on wing, and (*C*) on juncture between sides and wing.

(Legend continued on following page)

Jeswiet and his associates (*5, 6, 11, 30*), who used the hair groups in describing numerous cane varieties, believed them to be of great taxonomic value. De Calvino (*13*), on the other hand, considered the hair-group method of classification as an auxiliary method and of use to technically trained persons only. Neither the extreme confidence of Jeswiet nor the equally extreme attitude of De Calvino, which rests mostly on an analysis of conditions pertaining to only one variety (Cristalina), appears justifiable to the writer. To be sure, the usefulness of hair groups in the description and classification of sugarcane varieties is limited, but the method may be effectively used if the hair groups, as they occur, are coordinated with each other and with other characters.

To facilitate description and to make data readily available for comparison, it is often desirable to break up characters into as many fundamental units as possible. Jeswiet must have had this idea in mind when he listed the hair groups on the prophyllum, since their

(Continued from preceding page)

Hair groups on anterior side (fig. 4, *A*)

(1) Lateral groups on overlapping halves of prophyllum. Hairs are white, long, and cover the base of the bud to a greater or smaller extent.
(2) Basal groups on overlapping halves of prophyllum. These strips of short hairs are often interspersed with groups of longer hairs alternating with the veins and often covering the short hairs.
(5) Groups of straight or wavy, very appressed white hairs on one or both sides of the germ pore and usually associated with long buds.
(6) Bands of short brown hairs between the veins.
(9) A group of long lashes implanted in the germ pore on the inner side of the prophyllum.
(17) Groups of long, often wavy, appressed white hairs between the veins, giving the side a silky appearance.
(24) Short lashes along the upper half of the membranous margin.
(28) Incurved and downward-pointing hairs immediately above the germ pore on the posterior side of the prophyllum.
(30) Short, inward-pointing lashes on edge of germ pore.
(31) A group of long, white, downward-pointing hairs implanted at the point of insertion of basal appendage.
(32) Short brown hairs on the surface of basal appendage.

Hair groups on posterior side (fig. 4, *A*)

(10) Group of long hairs implanted on the tip of the side between the veins and possibly extending into region of wing. Hairs may or may not protrude above the bud.
(18) Strip of long white hairs along basal edge. The hairs may be long or very short, restricted to the center or distributed over entire basal curve. The hairs may form a compact row or small groups.
(20) Short brown hairs between the veins.
(23) Short brown hairs on tip, often masked by hairs of group 10.
(25) Long white hairs between the veins.

Hair groups on anterior wing (fig. 4, *B*)

(3) Long, white hairs on base of wing.
(4) Long, white, oblique or appressed lashes on edge of wing, limited to basal region or occurring over entire edge.
(12) Small, brownish hairs on surface of wing.
(13) Long, appressed hairs on surface of wing.
(15) Lashes at tip of wing; may be considered a part of group 4.

Hair groups on posterior wing (fig. 4, *B*)

(14) Long, appressed, white hairs on surface of wing; rarely found in *Saccharum officinarum*.
(21) Short, brown hairs on surface of wing.
(29) Long, white hairs on base of wing. Groups 4 and 15 shared with anterior of wing.

Hair groups on anterior juncture (fig. 4, *C*)

(7) Groups of short, brown, or long, white hairs above central germ pore.
(8) Long hairs appressed in regard to the wing or projecting above the wing.
(11) Long, wavy, white, appressed or protruding hairs on juncture of wing just beneath the wing tip.
(16) Groups of long white hairs implanted on a broad base in the basal depression between sides and wing.
(26) Long lashes in corners of the wing.

Hair groups on posterior juncture (fig. 4, *C*)

(19) Groups of long, white, and appressed hairs inserted in the basal corners and sometimes protruding above wing.
(22) A narrow band of appressed, long hairs, often forming a connection between groups 19 and 10. Group 26 is shared with anterior juncture.

number appears to be far larger than a conservative estimate based on fundamental types and regional distribution would warrant. A list of these small units, each designated simply by its number, should suffice when writing up descriptions. Jeswiet not only lists but describes the hair groups for each single variety.

Certain hair groups, as for example group 31, are found only in one restricted location. Others overlap, as for example groups 3 and 13, while some are definitely compound in that they include hairs from different groups.

Groups 1 and 2, fringing the basal part of the prophyllum below the insertion of the wing, are fundamentally one. The fact that the hairs of group 2 are at times short and straight instead of long and wavy is not important, because of the existence of many transitional types. Groups 5 and 17 are also fundamentally alike. Although group 5 is supposed to be located near the germ pore, Jeswiet's own illustrations often show the two groups intermixed. Groups 20 and 23 should be united, since the only difference between them is the restricted location of group 23. Groups 24 and 30 belong together, as already suggested by Jeswiet, and so, for similar reasons, do groups 4 and 15. Groups 3 and 13, on the anterior wing, and groups 29 and 14, on the posterior wing, are fundamentally the same, groups 3 and 29 being the basal parts of groups 13 and 14 respectively.

In studying the buds of a large and varied collection, one comes across forms where the natural regional grouping of hairs does not conform to the theoretical plan. Often the hairs of groups 3, 16, and 26, found on the basal part of wing and juncture, are grouped so closely as to form a single unit (fig. 5). The same arrangement often is found also in the corresponding groups, 19, 29, and 26, on the posterior side. Groups 11 and 10 are usually difficult to delimit. Group 11 very frequently contains elements of groups 13 and 17 (fig. 5); indeed, Jeswiet includes group 11 in group 13. This, however, may not always be done justly, since hairs of group 17 are frequently a component part of group 11. Group 10 shows probably the greatest amount of variatiom. There are some buds where group 10 is definitely implanted in the tip of the prophyllum. Often when the group is large, elements of group 25 are undoubtedly added; or, if the group is broad, elements of group 14 are included. Jeswiet refers to the fact that no equivalent for group 11 is found on the posterior side. Since in certain buds group 10 appears to be made up of two halves, it is possible that some elements of the two halves are the missing group.

The status of the hairs in the germ pore, groups 9, 28, and 30, does not seem very clear. Group 30 should be considered as belonging to 24, as already suggested by Jeswiet. Group 9, as described by Jeswiet, has never been observed by the writer. Not infrequently, however, long hairs have been seen issuing from the germ pore, but these hairs always belonged to the anterior part of an enclosed leaf. Group 28 is supposed to be inserted in the hollow of the prophyllum just above the germ pore and may be just a modification of group 30, i. e., a part of group 24, which is the general designation for hairs fringing the membranous border of the overlapping half of the anterior side.

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In a number of varieties the overlapping margin near the germ pore is covered with long, dense hair (fig. 5). These hairs may be a continuation of group 24, but they differ from that group not only

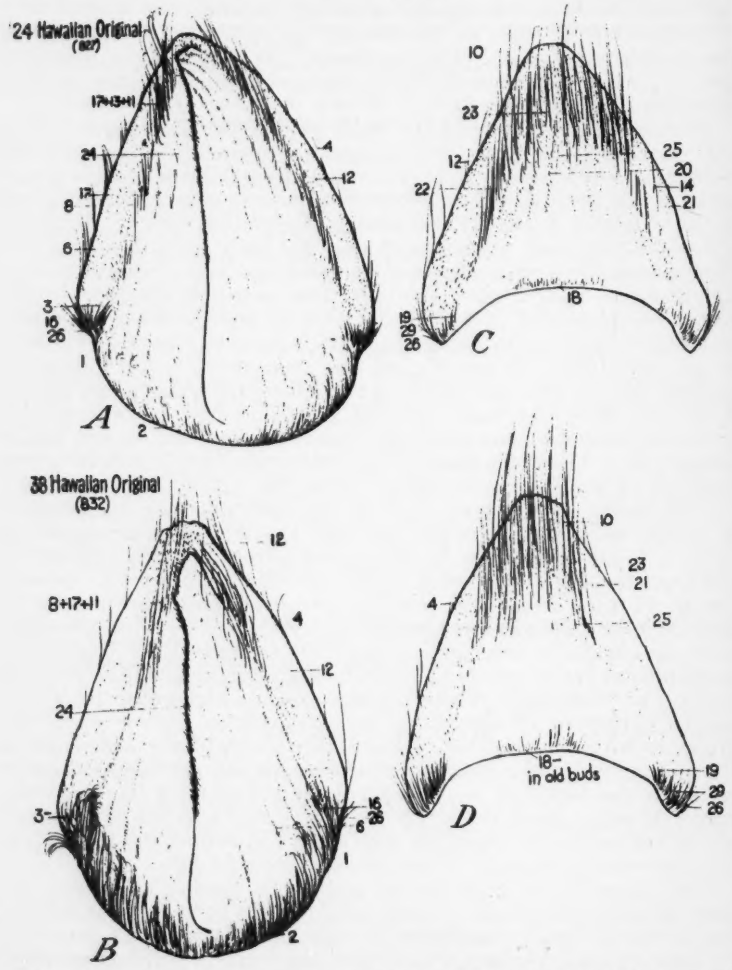
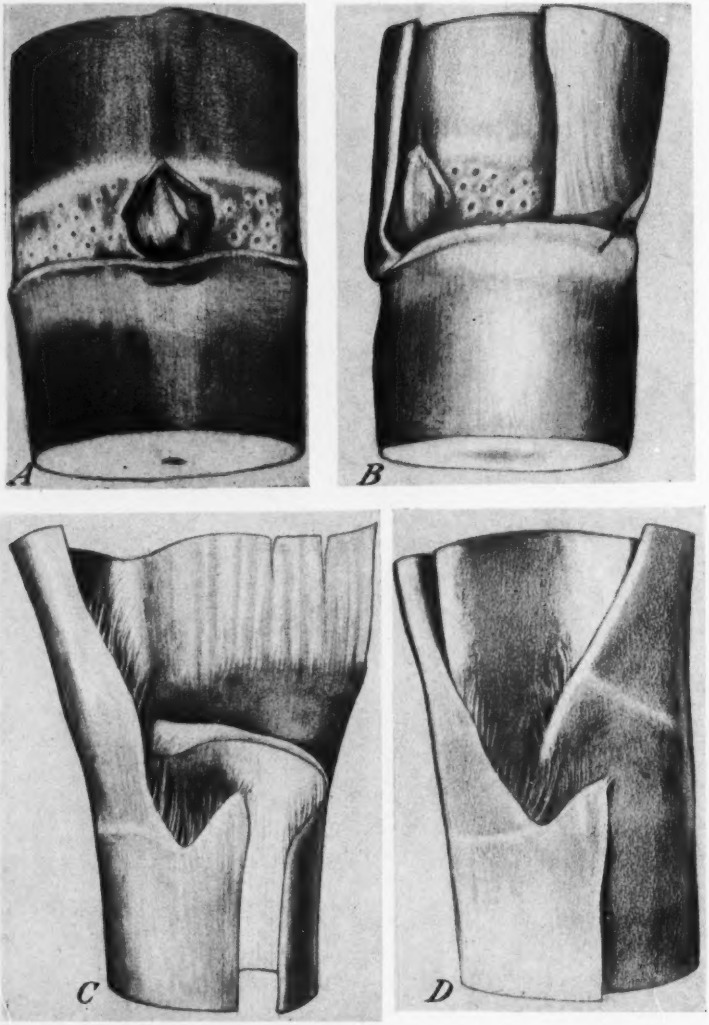


FIGURE 5.—Buds of two Hawaiian Original varieties with typical hair groups on anterior (*A*, *B*) and posterior (*C*, *D*) sides of prophyllum. × 6.

by their greater length but also by their distribution, not being limited to the margin but covering a prominent band near the margin. They do not seem to fit any of the known groups and should be given a separate number unless the limitation of group 24 is less restricted.



A, Structure of nodal region. Bud inserted at scar; growth ring narrow. *B*, Structure of nodal region with sheath partly cut away to show relation of parts. *C*, Structure of blade joint with ligule. *D*, Structure of blade joint in natural position; outer auricle small and deltoid. All × 1½.

MORPHOLOGY OF THE LEAF

In general appearance, the leaves of sugarcane are like those of other grasses. They are borne on the culm in two ranks, one at each node. The number of leaves on a stalk varies with the variety. As new leaves progressively unfold, old ones are shed, so that the number remains approximately constant throughout the vegetative life of a stalk.

Each leaf consists of sheath and blade. At the juncture of sheath and blade is the blade joint with its specialized regions (pl. 6, *C*, *D*); while at the base of the sheath, where the leaf joins the stalk, there is a distinct swelling—the leaf sheath node or sheath base (pl. 6, *B*).

LEAF BLADE

General Morphology

Leaves when immature are usually stiff and erect. They may retain this position on maturing except that the tips may droop. Most often the blades are ascending; in some varieties, they spread fanlike in a gentle curve.

The blades may be long and narrow or relatively broad, tapering toward the apex, often ending in a long, fine point. There are canes in which the lamina is regionally reduced to the width of the midrib. In these varieties the blade is narrowest where it joins the sheath; it gradually broadens and tapers again toward the apex. Many leaves are relatively broad at the base; they retain this width to a point just below the middle of the blade; from there on the width gradually decreases upward toward the tip. Length and width vary greatly and do not constitute a reliable character. But the ratio of length to width was found to be constant by Panje (*29*) for varieties of *Saccharum spontaneum*, and this relationship probably holds true for other groups.

The color of the blade is commonly a medium green, parts that are much exposed to the sun showing a reddish cast. In some varieties, especially in the juvenile stage, the color is decidedly reddish or purplish. If much wax is present, the lower surface appears bluish. In varieties with Chunnee blood, according to Jeswiet (*15*), the dark-green surface of the blade is usually dotted with yellow patches. There are canes in which both the upper and the lower surfaces are covered with a pronounced velvety pubescence; in these, the color of the blade is gray, often with a reddish cast.

The blade is divided by the midrib into halves that are asymmetrical, since the part of the blade that corresponds to the underlying part of the sheath is usually broader than the other half. The midrib is usually prominent. In some varieties it is thick and heavy, in others flat and inconspicuous. Its lower surface is usually dark green, in some varieties marked with a lighter stripe that runs along the center. In the varieties of *Saccharum spontaneum* the midrib is usually white on the upper surface, or lighter green than the lamina. The upper surface of the midrib is channeled, while the lower side is convex near the base. The midrib is always widest at the base and gradually tapers toward the apex; at times, it fades altogether before reaching the tip of the lamina.

The veins run parallel to the midrib. They are of different thickness, a fact apparent to the naked eye in some varieties but more readily recognized with the aid of a microscope in others. In some leaves the lamina looks conspicuously ribbed; in others, not even the larger primary veins project above the leaf surface. The structure of the veins and its relation to the epidermal pattern will be discussed below.

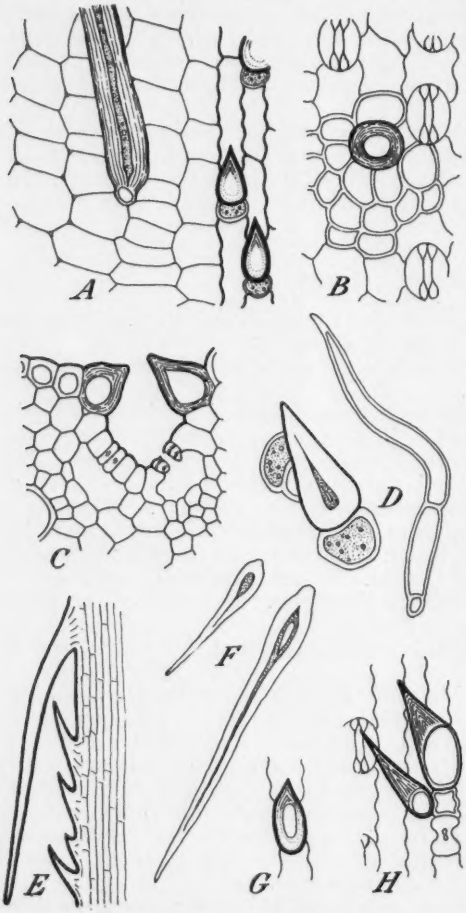


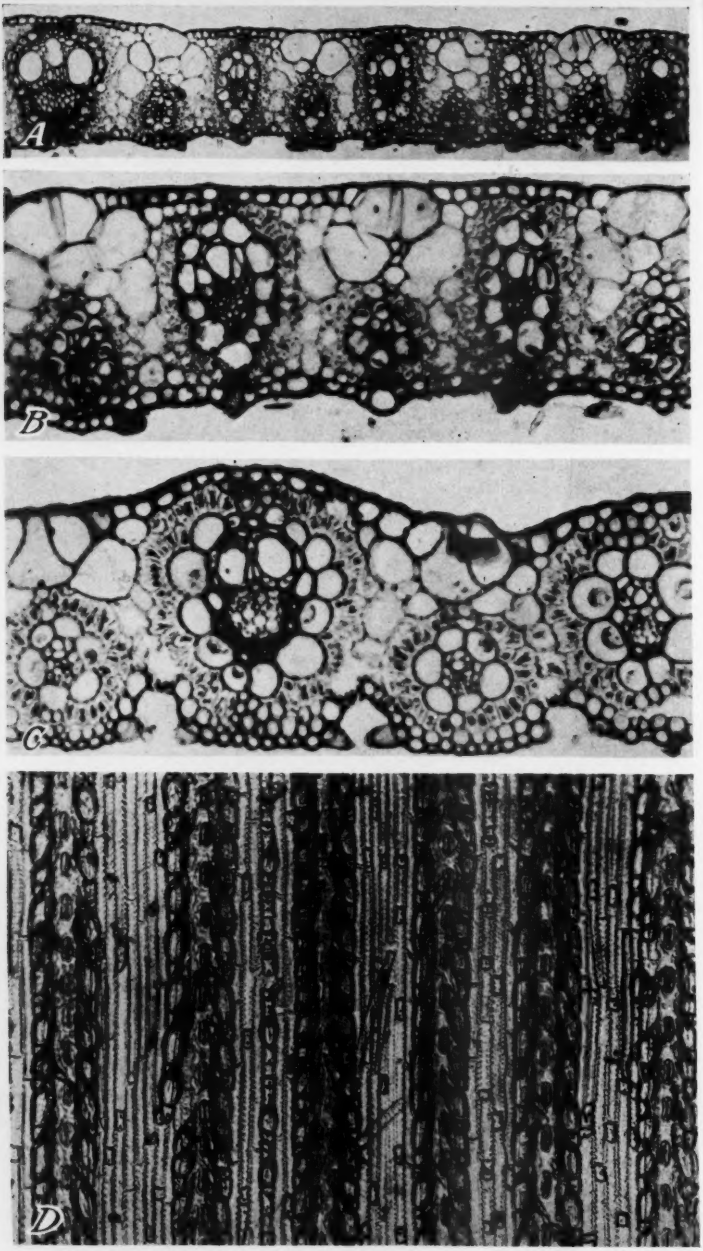
FIGURE 6.—Hairs and spines on leaf and sheath: *A*, Surface view of bulliform zone of the upper epidermis of the blade; in the center is shown the base of a velvety hair (group 67); at the right, cells from marginal zone with short spines. × 300. *B*, Same as *A* but taken from lower epidermis; cells surrounding base of hair are very thick-walled. × 300. *C*, Stomatal groove in lower epidermis of *Saccharum spontaneum*. × 480. *D*, Short spine and two-celled hair from leaf sheath. *E*, Spines from edge of leaf blade. *F*, One-celled hairs from dewlaps. *G*, Solitary spine from midrib region of lower epidermis of blade. *H*, Clustered spines from the lower epidermis of the blade.

Although little information concerning texture of leaves is to be found in varietal descriptions of sugarcane, there exists much variation between different varieties. Even to the casual observer, some leaves appear thin, others heavy; some feel smooth, others rough to the touch; some leaves appear leathery, others relatively succulent.

PUBESCENCE

The microscopic pubescence of the leaf will be described in detail in the discussion of the structure of the leaf epidermis. In addition to this, there are two hair groups, designated by Jeswiet as groups 53 and 67, which are readily visible to the naked eye. Group 53 (fig. 6, *E*) is always present, though not always prominent, while group 67 is relatively rare.

The hairs constituting group 67 are found in the intercostal region



A, Cross section of leaf, showing large and small bundles regularly alternating with one another. × 160. *B*, Cross section of leaf enlarged, showing two types of bundles; notice bulliform cells in upper epidermis. × 320. *C*, Cross section of leaf of *Saccharum spontaneum*, showing stomatal grooves in lower epidermis. × 240. *D*, Surface view of *S. spontaneum*, showing rows of spines converging over sunken stomata. × 190.

of the lower surface and in the zone of bulliform cells of the upper surface (fig. 6, *A*). They are relatively large, long, and soft, as in 28 N. G. 38, Imp. 477, or, occasionally, very stiff. The base of these hairs is raised and is composed of more or less concentrically arranged cells. The walls of these cells are thicker and more heavily silicified than those of the neighboring tissue (fig. 6, *B*). The hairs are always most abundant in the region just above the dewlaps, and denser near the midrib than at the leaf margin. The margin itself is protected by stiff ascending bristles (group 53). In the region just above the blade joint, these hairs are long and relatively soft; higher up, they are short and stiff and often form double rows.

Epidermal Structure

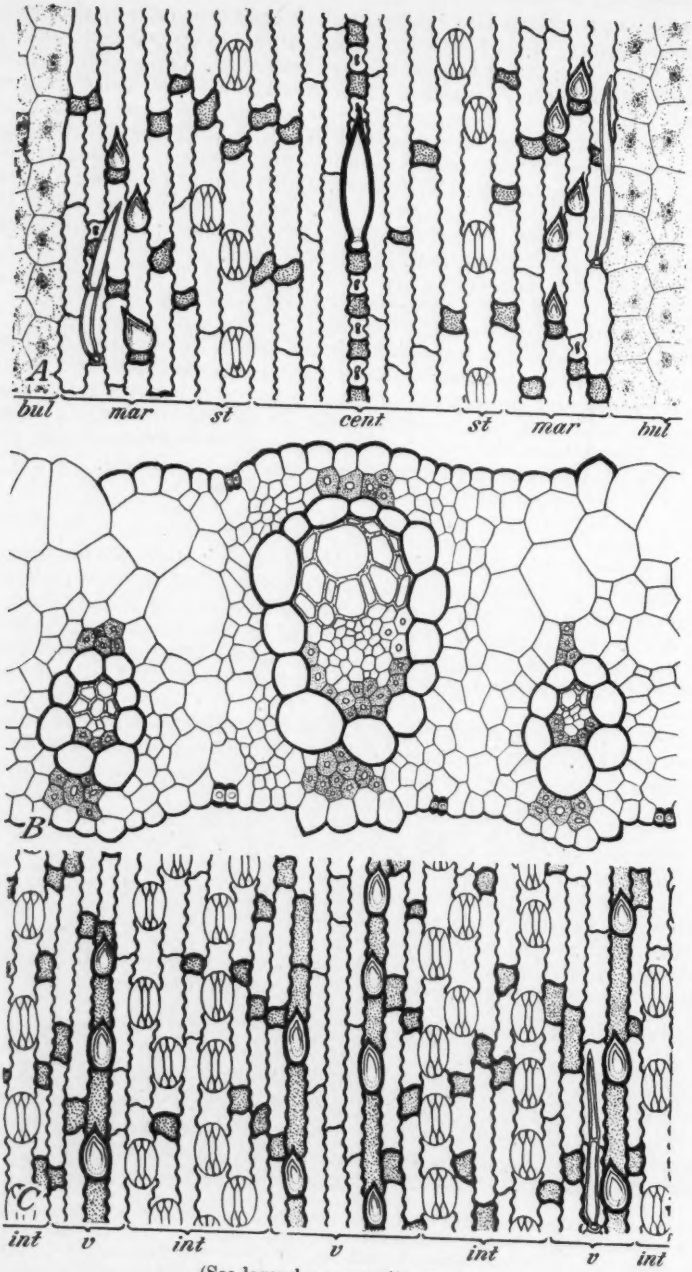
The elements of the leaf epidermis are essentially those of the stem, except that they are modified so as to adapt them to the function of assimilation and protection. In both stem and leaf we recognize a definite epidermal pattern, but, while the stem structure is homogeneous throughout, the leaf shows a periodically recurring design that is related to the tissue elements underlying the epidermis.

CROSS SECTION OF LEAF

An understanding of the inner leaf structure is desirable for the recognition of this relationship; to facilitate it, a leaf cross section with the corresponding lower and upper epidermis in face view is given in figure 7. It will be seen from a study of the cross section that groups of epidermal cells alternately abut on sheath cells and parenchyma cells and that the upper leaf surface has, in addition, bands of bulliform elements usually several cells wide. The cross section shows further that there are bundles of different sizes that alternate with one another. Bundles larger than those shown in figure 7 occur at greater intervals and these alternate with still larger bundles (pl. 7, *A*, *B*). The latter form the primary veins of the leaf and are readily seen with the naked eye, being thicker than the intercostal area and projecting as more or less prominent ridges. Altogether, there are veins of three or four different magnitudes, occurring at regular intervals. All the veins are structurally similar; all except the smallest have two sclerenchyma caps abutting on the lower and upper epidermis. The xylem cap of the smallest veins does not reach up to the upper epidermis but borders on a group of bulliform cells of which the outermost are an integral part of the epidermal structure.

LOWER EPIDERMIS

The surface view of the lower epidermis of the blade (fig. 7, *C*) shows longitudinally running bands of cells of different designs alternating with one another. The position of these bands, as seen in the adjacent cross section (*B*), shows a definite relationship to the type of cells underlying them.



(See legend on opposite page)

Most conspicuous are the bands containing stomata. They are approximately three rows wide and consist of stomata alternating with long cells. At times, the rows of stomata are completely or partly separated from one another by a row of long cells alternating with groups of short cells.

The stomatal bands are flanked by strips of long, narrow cells that overlie the sclerenchymatous bundle caps. As the bundles, which alternate with one another, vary in magnitude, the number of rows constituting the tissue between stomatal bands differs accordingly. The narrowest bands are made up of just a few rows of elongated cells that may be separated from one another by cork cells or cork and silica cells. Bands overlying the large primary veins are much broader. The middle row of such a band and sometimes two adjacent or closely adjoining rows are made up entirely of groups of short cells.

In addition to the cells mentioned, the lower epidermis of the blade has one or several types of hairs. Always present, though in varying numbers, are appressed two-celled hairs, which are most commonly found among the cells bordering the bands of stomata and occasionally scattered among the stomatal rows. Not always present but sometimes exceedingly numerous are short spines (fig.6, *G, H*), either associated with the two-celled hairs or more usually restricted to the bands of long cells overlying the veins. The spines most often point upward in the direction of the longitudinal axis, but they may be variously oriented. They may be entirely wanting or they may occur in such large numbers as to form one or several uninterrupted rows. Most significant is their presence in certain varieties of *Saccharum spontaneum*, where the stomata are sunken, forming the so-called stomatal grooves (pl. 7, *C, D*, and fig. 6, *C*). Their occurrence has been associated with varietal resistance to mosaic (*32*), since, wherever they occur, plant lice have no access to the stomata. In this connection, however, it is well to remember that stomata are also found on the upper leaf surface, where they are not similarly protected.

UPPER EPIDERMIS

Except for the added presence of bulliform cells, the elements making up the upper epidermis are the same as those found in the lower though in different proportions. The bulliform cells are easily the most outstanding structural characteristic of the upper epidermis. Depending, as a rule, on the relative size of the veins and their spacing, the bands of bulliform cell rows are wide or narrow, crowded or far apart. The cells themselves often differ with the variety. In some varieties, they are of a honeycomb pattern; in others, they are squarish, somewhat elongated, or broader than long.

The tissue enclosed by the two bands of bulliform cells is for convenience divided into several zones, for which details are given in the composite drawing of cross-section and surface views (fig. 7).

FIGURE 7.—*A*, Surface view of upper epidermis of blade. × 320. *bul*, Bulliform cells; *cent*, central zone; *mar*, marginal zone with two-celled hair and short spines; *st*, stomata. *B*, Cross section of leaf; different types of epidermal cells more or less in juxtaposition with their kind in surface view. × 320. *C*, Surface view of lower epidermis. × 320: *int*, Epidermal tissue overlying intercostal region; *v*, epidermal tissue overlying veins.

Adjacent to the bulliform bands and limited on the other side by one row of stomata is a tissue that may be called the marginal zone. It is from one to five cells wide and contains two-celled hairs and spines. The two-celled hairs are always present, though in varying numbers, and are usually found in the row directly adjacent to the bulliform cells. Spines are absent from some varieties; in others, they may be scarce or abundant. The marginal tissue itself is composed of long cells alternating with short groups that often lack silica cells. Wherever hairs or spines are present, they take the place of silica cells in the short group.

Stomata occur normally in single rows; sometimes their distribution is somewhat staggered, giving the impression of two rows. In some of the wild canes, Shantir Barhni (*Saccharum narenga* Wall.) for example, there are two and even three rows of stomata.

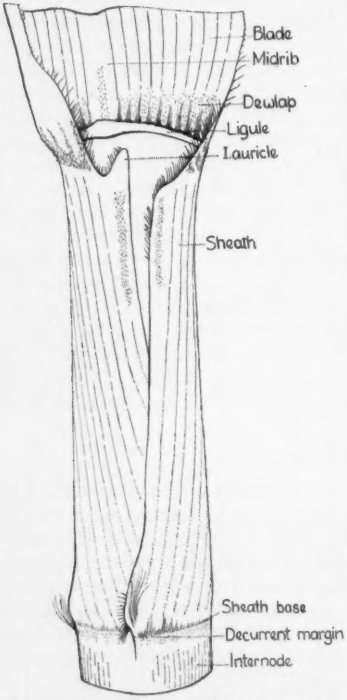


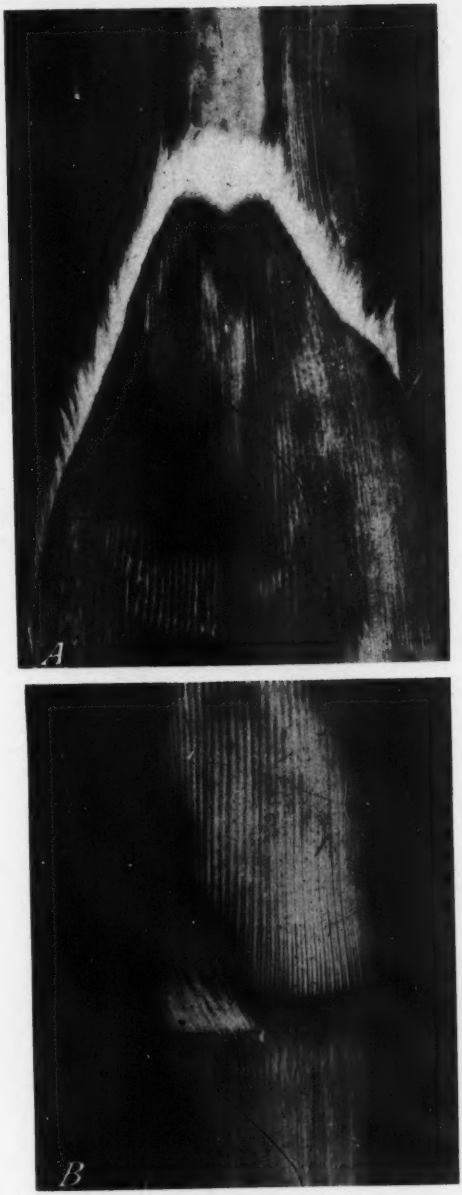
FIGURE 8.—Structure of sheath. To show the parts of the blade joint, the sheath is drawn without the part of the stem that it normally encloses.

The relatively broad band of tissue between the rows of stomata, the so-called central zone, is composed of elongated cells or long cells alternating with short groups. Frequently the long cells are found in uninterrupted rows, and often the silica cells are wanting from the short groups. The central zone is frequently divided by a narrow band of uninterrupted short cells, composed of cork and silica cells alternating with one another. Sometimes a few of the silica cells are replaced by short spines. These may become very large as compared to the surrounding cells. Such giant spines are frequently found in the upper epidermis in varieties of *Saccharum spontaneum* (fig. 7, *A*). Where the tissue enclosed between two bands of bulliform cells is rather narrow, the central zone lacks the rows of short cells and the marginal zone is only one or two cells wide.

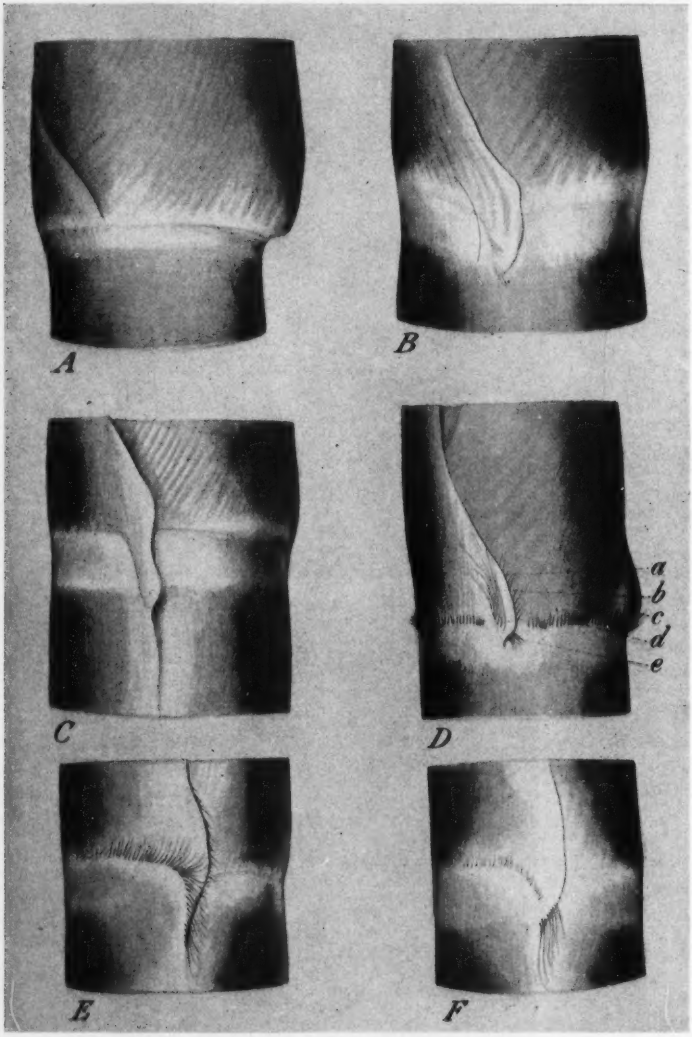
LEAF SHEATH

General Morphology

The leaf sheath envelops the culm above the node and forms an open tube with the margins overlapping (fig. 8), the overlying margin being alternately the right and the left in successive nodes. Flattened out, the sheath represents a rectangular surface, slightly contracted where it joins the lamina below the blade joint and flaring out where it envelops the node (fig. 9). The degree of overlap varies greatly and is not a fixed char-



A, Structure of blade joint of Teboe Glongong (*Erianthus arundinaceus*). Note the narrow leaf blade, the steeply sloping ligule with dense pubescence back of it and pseudo-midrib of sheath below ligule. *B*, Sheath base region of same variety. Tissue of sheath joint darkly discolored. Hair group 59 prominent in sector adjoining overlying sheath margin.



A, Structure of sheath base: Straight, somewhat saccate, and overlying sheath margin not decurrent. *B*, Overlying sheath margin decurrent and appendaged. *C*, Overlying sheath margin prominently decurrent. *D*, Pubescence of sheath base region: *a*, Hair group 64; *b*, hair group 62; *c*, hair group 69; *d*, hair group 59; *e*, separate group, generally considered as belonging to group 64. *E*, Overlying sheath margin decurrent; prominent hair group 64 and partially developed group 59, which in region of sheath margin joins with group 64. *F*, Decurrent and appendaged sheath margin with prominent tuft of hair on lowest tip. This group corresponds to *e* of figure *D*.

acter. Usually the circumference of the leaf sheath at its base is about one and one-third times, in wild varieties up to one and one-half times, that of the stem.

The length of the sheath differs with the variety—from 15 to 52 cm. in the varieties studied—but within varietal limits it is fairly constant.

The sheath is thickest medially and often bulges, saclike, just where it covers the bud (pl. 6, *B*). It is thinner toward the margins, forming near its base a wide or narrow membranous border, which on maturity becomes dry and brown.

The sheath, like the lamina, contains many parallel veins, but these are more widely spaced than in the blade. They are largest in the median part, gradually becoming smaller toward the edges. Usually there is no midrib, although in Teboe Glongong (*Erianthus arundinaceus* (Retz) Jeswiet) the midrib of the blade extends into the upper part of the sheath (pl. 8, *A*).

The sheath is inserted in the tissue of the node, forming an even line around the stalk (pl. 9, *A*). In many varieties the overlying edge of the sheath runs down the stalk, often ending in an inconspicuous or a more or less prominent appendage (pl. 9, *B–F*).

The region immediately above the line of insertion of the sheath is called the leaf-sheath node, or sheath base. It is a zone of meristematic tissue, from which the sheath elongates, and is comparable to the growth ring of the stem. Structurally it reflects the molding influence of its location, which demands great elasticity of tissues combined with late maturing. This region possesses increased flexibility, attained by replacement of the sclerenchymatous elements in the vascular bundle sheaths by collenchyma, and also greater strength due to small-celled parenchyma occurring in regions where large air cavities are usually found. When the sheath is fully grown though still young, the sheath base is set off from the rest of the sheath by a differential color, generally yellow orange or yellow green. In varieties that retain their leaves, commonly in wild canes, this color darkens as the leaf ages (pl. 8, *B*).

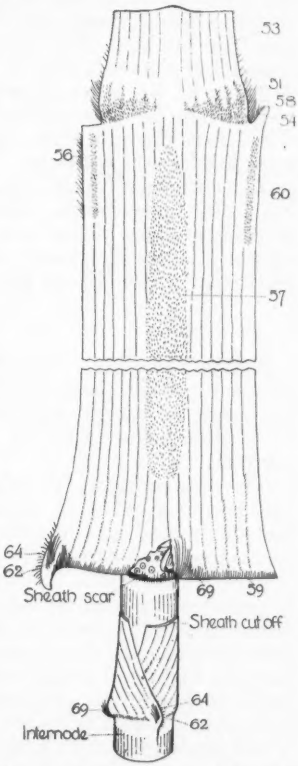


FIGURE 9.—Surface view of sheath, showing location of hair groups.

In canes where the stem cleans itself naturally, the sheath base of old leaves disintegrates, and when a leaf drops off, a scar remains (pl. 6, *A*). In most varieties, the scar is at right angles to the internode though it may be oblique to the axis of the culm, or the leaf scars are

somewhat oblique in relation to each other. In some forms the scar is even, small, often closely appressed to the stalk on the side opposite the bud, and in others, especially in canes with pronounced saccate sheaths, the scar is squarrose and often sags and spreads under the bud (pl. 4, *C*).

The color of the leaf sheath is usually light green, sometimes flushed with dark red or purple. The sheaths when young often have a purplish hue; later they may be green. The edges of the sheath are translucent, or they may be reddish. In some striped canes, the color pattern extends into the sheath and, in variegated leaves, even into the lamina. The dark stripes of such canes are usually produced by pigmentation of all layers immediately beneath the epidermis; the white bands are due to regional lack of chlorophyll.

Wax may be deposited uniformly and profusely all over the sheath. Some varieties are only slightly or not at all waxy. Wax deposits vary locally and with age.

The surface of the sheath is smooth or covered with a vestiture of hair. In some canes, hairs are present only on the first-formed sheaths whereas in the later ones the surface is glabrous. The hairs of the unexposed sheaths are much appressed, becoming declinate, especially in the upper region, when the sheath is exposed.

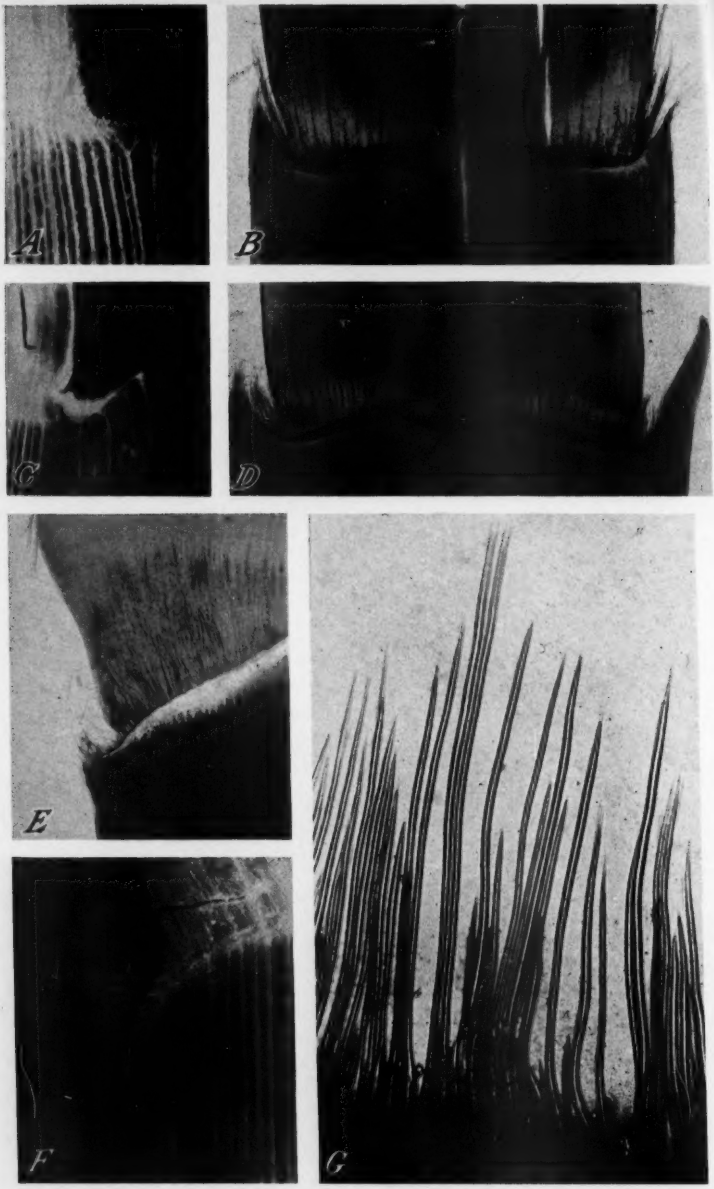
Pubescence

Just as some buds are entirely clothed with hair, some sheaths are also completely covered. Most often, however, the hairs are concentrated in certain regions which have been delimited by Jeswiet (*15*), who made extensive use of them in his description of cane varieties.

The numbering of the hair groups on the sheath as given by Jeswiet (*15*) has been retained, but, as in the case of the bud, changes have been suggested and illustrations have been introduced wherever it seemed necessary to clarify the situation.

Jeswiet group 57.—According to Jeswiet, this group is of greatest importance in making determinations. It is found in many cane varieties and it covers the outer surface of the sheath to a greater or lesser degree. In some canes, this dorsal field is very small, is usually inserted high, and consists of only a scanty covering of hairs. Other similarly implanted patches are narrow at the base and then broaden out. Some dorsal fields are implanted low and extend up to the region of the blade joint. In a few canes there is only a small central patch, either linear or lenticular in shape, while in others the field is very irregular and in places so broad as to encroach on the membranous border. The hairs of the dorsal patch may be sharp and long—up to 4 mm.—or relatively short and then usually associated with weakly developed fields. The hairs are almost always inserted obliquely, often appressed but at times almost erect in the upper region of the patch.

Jeswiet group 60.—The two hair groups on the sides of the leaf sheath, the lateral patches, often occur together with the dorsal group, but they are found in fewer varieties. The arrangement on a given sheath is often asymmetrical. Sometimes the lateral field of



Structure of ligule and auricles. Color values are reversed, since photographs were taken directly on paper. *A*, Small outer auricle of Chunnee, showing prominent venation and long cilia on upper free margin (hair group 54). × 3. *B*, Symmetrical cresent-shaped ligule, rather tall and not sloping; both auricles inserted high and on the same level. × 1½. *C*, Small deltoid auricle with ciliate free margin. Projecting hairs on outer surface belong to groups 56 and 60. × 3. *D*, Arcuate type of ligule. Inner auricle large and lanceolate, outer one small and deltoid. × 1½. *E*, Inner surface of dewlap with well-developed hair group 52 and inconspicuously developed group 51; auricle very small and of transitional type. × 1½. *F*, Flank of ligule steeply decurrent; auricle absent. × 3. *G*, Long cilia (group 61) on margin of ligule of Kassoer cane. × 65.

the overlying margin is very small, consisting of only a few rows of hairs, while the field on the underlying margin is well developed. The lateral patches are practically always inserted high and usually terminate immediately below the dewlaps. In some varieties, for example Hinds Special, the lateral field of the inner sheath margin extends onto the auricle, a condition which is even more pronounced in some wild canes (Shantir Barhni). Here the pubescence is so dense all over the sheath that no separate groups can be recognized. In variety 28 N. G. 49, the lateral patch broadens just below the collar, forming quite a conspicuous fringe at the basal margin of the dewlaps. Sometimes the lateral patches are rather long, extending over three-fourths of the length of the sheath. They are usually very narrow and remain linear, or they may flare out some distance above their insertion and even partly fuse with the dorsal patch. The hairs of the lateral patches are in length and general character like those of the dorsal patch.

Jeswiet group 56.—This group consists of long or short lashes on the upper part of the sheath margin. In wild canes, where this character is best developed, prominent lashes are found on both margins. The group is wanting in most noble canes and is only weakly developed in some of the hybrids between *Saccharum officinarum* and *S. spontaneum*. Apically the group occasionally abuts on and becomes continuous with the marginal cilia of the auricle (pl. 10, *C*). In some varieties with pronounced lateral patches in which the hairs crowd up to the margin, the cilia of group 56 become inseparably mixed with hairs of the lateral patch.

A casual examination shows that the region of the base of the sheath is usually smooth, though there are frequently a few small, fairly well-defined hair groups present. Some of these groups belong to the leaf-sheath base. These often stand out most clearly in young leaves, and sometimes they are conspicuous after the leaves are shed. Other groups are found on the surface and margin of the decurrent basal part of the sheath.

According to Jeswiet's description, group 62 consists of silky long hairs covering the lowest tip of the overlying sheath margin, found frequently in seedlings containing Chunnee blood. Group 64 is found in the same region, forming lashes at the lower end of the margin. Jeswiet provides no illustrations for these groups, and his descriptions do not always localize the groups sufficiently for clear diagnosis.

The material examined in the course of these studies shows group 62 as a rather inconspicuous accumbent patch of fairly long, soft, sometimes feltlike hair (pl. 9, *D*). The basal part of the decurrent margin is occasionally ciliate, and the cilia are easily recognized as group 64. Frequently, however, a third group of downward-declinate cilia is seen immediately above the insertion of the basal appendage. Jeswiet refers to this corner group in some of his descriptions but includes it, as the case may be, sometimes under group 64, sometimes under group 62. Because of its frequent and localized occurrence it should, perhaps, be given a separate number.

Some cane varieties often show a distinct pubescence on the sheath base. The hairs are short, medium long, or very long, and usually point upward, being either appressed or slightly ascending. The

hairs may form a complete or a broken circle. Often they are most numerous and long in that part of the circle which overlies the bud; because of this regional prominence, Jeswiet treats them as a separate group under No. 69. However, on the opposite side of the bud, in the immediate vicinity of the overlying decurrent sheath margin, a similar concentration of hairs occurs in some varieties (especially conspicuous in Teboe Glongong, pl. 10, *B*), which bears no separate number but is treated under group 59. For the sake of consistency, this tuft should also bear a separate number, or else there should be no division at all made in the original group.

Sometimes the hairs found in the intercostal region of the sheath base, which will be mentioned again in the study of the epidermis of the sheath, are especially prominent, simulating a weakly developed group 59. Sometimes the hairs are short and black and extend lower down into the wax band of the internode below. In canes where this condition is pronounced, it constitutes a valuable character.

Epidermal Structure

The epidermis of the sheath, like that of the blade, overlies two specialized regions: intercostal area and vein tissue. The intercostal areas of the sheath are much broader than the corresponding areas in the lamina, and the epidermal pattern is much more regular.

The epidermis overlying the intercostal region consists of regular long cells alternating with groups of short cells (fig. 10, *A*). Hairs are of frequent occurrence. The two-celled type (fig. 6, *D*) is always present, though in varying numbers, being most abundant in the region above the sheath base and sparsest in the apical region. Different varieties differ as to the relative distribution of these hairs. In some, the hairs are few; in others, they form a feltlike covering. Short solitary spines are also often found in combination with groups of short cells (fig. 6, *D*) or occurring singly between two long cells. In addition to the short spines, there are relatively large spines present, making up groups 57 and 60, which have been described in an earlier section.

The epidermis overlying the vein tissue is separated from the intercostal region by a single row of stomata which may be locally staggered, giving the appearance of two rows. The epidermal tissue of the vein region may consist of either one or two types of cell rows: rows made up of very long cells (fig. 10, *B*) which may alternate with short groups, or rows made up entirely of cork and silica cells (fig. 10, *C*). One or the other type predominates, depending on the variety. In some canes, there is a large number of adjacent rows composed of short cells only; in others, a few long cells are interpolated within the rows. Frequently bands consisting of rows of short cells are separated by narrow bands or solitary rows of long cells. In some cane varieties the entire vein area is overlaid by long cells, while in others there are bands of only short cells, often bearing solitary declinate spines. The occurrence of spines in this zone is a varietal character. The spines may be few in number and scattered or rather numerous and then in more or less broken rows. They point occasionally in the direction of the vertical axis, though more often they are obliquely declinate.

There is a slight consistency in the distribution of certain elements of the epidermis of stem, sheath, and lamina.

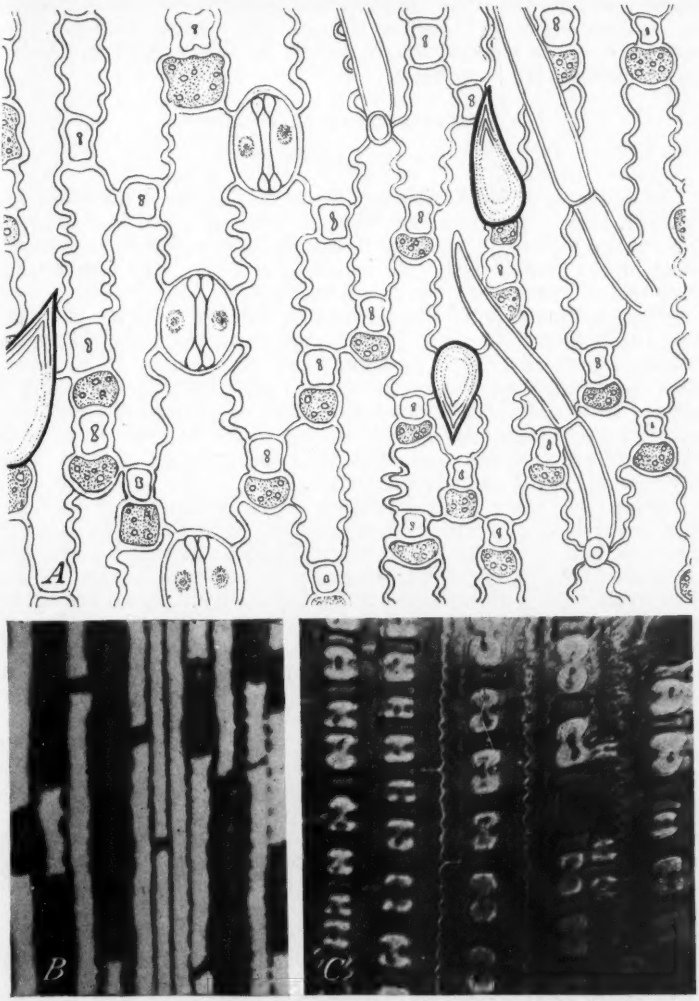


FIGURE 10.—*A*, Epidermal tissue overlying intercostal area of sheath, × 500. *B*, Tissue from region overlying vein: rows of short cells alternate with rows of very narrow elongated cells, × 300. *C*, Tissue from region similar to *B* but from another variety; practically the entire tissue is composed of short cells, × 320.

BLADE JOINT

Blade joint is the name given to that part of the leaf where the lamina joins the sheath (pl. 6, *C*, *D*). The inner surface of the blade joint is known as the throat; it is limited basally by a membranous ap-

pendage called the ligule. The region forming the back or outer surface of the blade joint is the collar. It is composed of two somewhat triangular areas that differ in color and texture from the surrounding tissue; these areas are known as the dewlaps, or joint triangles. Projecting from the sheath margin below the blade joint are pointed appendages known as auricles.

Dewlaps or Joint Triangles

General Morphology

The dewlaps, or joint triangles, form the flanges of the blade joint (fig. 11). They are provided with folds which give the leaf mobility. Structurally the vascular tissue in this region resembles that found in the sheath base. As in the latter, the large bundles have much collenchyma while the xylem consists of spiral vessels.

Although the shape of the dewlaps on successive leaves of a stalk, from the youngest to those fully grown, may vary, there is, nevertheless, a prevailing type pattern. For comparison it is best to select leaves that are mature or almost fully grown and in which the dewlaps have not suffered from the effect of adverse environmental conditions by becoming frayed at the edges or even torn. Also, because of a pronounced asymmetry in the structure of most leaves, only related sides should be compared.

Dewlaps belonging to the youngest leaves are usually of a different color from those of mature organs, though sometimes the color difference is one of degree rather than of kind. Many dewlaps when young are at first a bright red; when mature, a bronze brown. Others when young are yellow; later, a shade of olive. Some are at first grass green, turning to yellow green or olive on maturing. In some varieties, the color of mature dewlaps is brownish or almost black, often modified by the presence of wax or hair. The dewlaps are usually colored uniformly but in some varieties they are prominently edged with yellow or a tint of red.

The outer surface of the dewlaps is more or less heavily waxed, the inner surface less so. The amount of wax deposit varies from a faint bloom to a heavy layer that often hides the natural color or greatly alters it through discoloration upon aging.

In the narrow-leaved wild canes, the dewlaps are always triangular, the apices of the triangles almost meeting on the back surface of the midrib. There is a great variety of forms in the broad-leaved noble canes, but these may be readily assigned to one of three basic groups—the rectangular type, the deltoid or triangular type, and the ligular type (fig. 11, *A–I*). There are many intermediary forms that tend to bridge the difference between the three patterns.

The shape of the dewlaps is influenced by the slope of the ligule, which marks their lower boundary. In practically all young dewlaps and in many mature ones, the base runs horizontally either in a straight or curved line (fig. 11, *I*); it may also be more or less undulate. It may have the same outline as the lower margin (fig. 11, *I*), or there may be a depression in the upper margin in juxtaposition with an elevation in the lower. The outer dewlap margin extends between blade and sheath, and its curve influences the shape of the dewlap. In some varieties, the blade and dewlap margin forms a straight

vertical line; in others, the dewlap has a slight bulge or a depression (fig. 11, *H*) often just above the termination of the ligule and most pronounced on the dewlap corresponding to the overlying sheath margin.

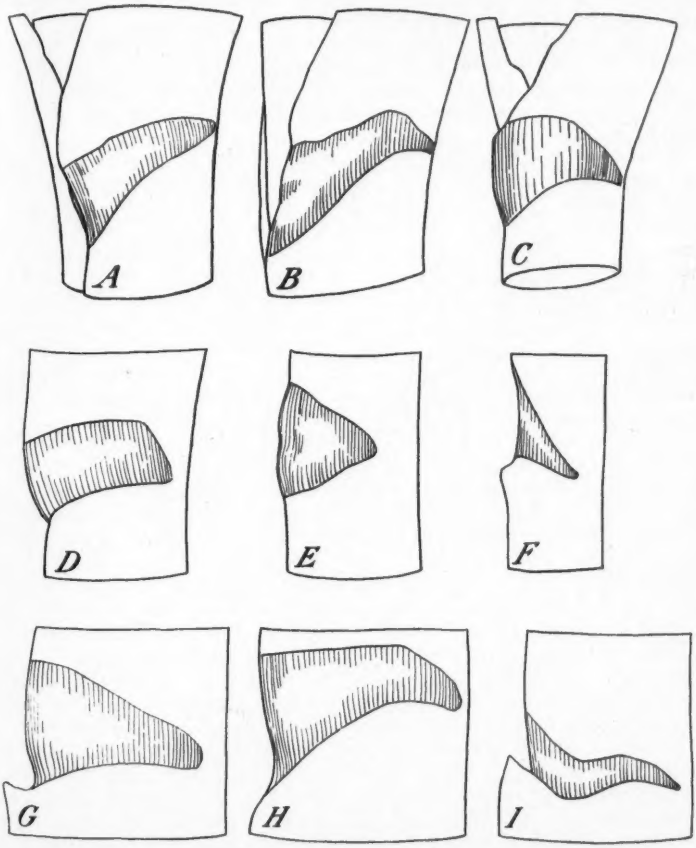


FIGURE 11.—Types of dewlaps: *A*, Very sloping, narrow triangular-ligulate dewlap, Hawiian Original 24; *B*, very sloping, more or less ligulate dewlap, Louisiana Striped; *C*, tall triangular dewlap with convex upper and lower margin, Rayada; *D*, squarish type of dewlap, Tekcha; *E*, typical deltoid dewlap, Hatooni; *F*, triangular dewlap of the type found in varieties of *Saccharum spontaneum*; *G*, triangular dewlap with horizontal basal margin; *H*, more or less triangular, sloping dewlap with horizontal upper margin, Striped Mauritius; *I*, typical ligulate dewlap, very narrow and practically horizontal, 28 N. G. 251.

PUBESCENCE

The dewlaps have a sparse, dense, or even feltlike pubescence, which is almost always more prominent on the inner or dorsal surface than on the outer or ventral side. The degree of hair development is often in inverse ratio to the amount of wax deposit. The

outer surface is usually heavily waxed, while the pubescence is inconspicuous. On the other hand, the inner surface, which rarely has a prominent layer of wax, is usually very hairy.

The prominent venation of blade and sheath is lacking in the dewlap region, yet the distribution of hairs shows a definite banded pattern, especially on the inner surface.

In the designation of the pubescence of the dewlaps, Jeswiet's hair group numbers have been retained. There is no overlapping of groups except for the cilia of the outer dewlap margin in varieties where the marginal zone of the ventral surface has the long type of hair.

Jeswiet group 58.—The outer surface of the dewlap is, as a rule, only moderately covered with hair, and in some varieties it is practically glabrous. The hairs (fig. 6, *F*) are short, unicellular, and, in mature organs, often hidden under a layer of wax. The entire surface may be uniformly covered with hair or the pubescence may be restricted to the marginal zone. In some varieties, the surface has a dense, feltlike covering and the hairs are uniformly short. In other varieties the hairs are longer near the edges, where they form long marginal cilia. A band or tuft of long hairs is found at the base of the dewlaps in New Caledonia 11 (fig. 14, *E*) and in certain wild canes. The hairs are more or less continuous with those of group 60, if this group is present, covering up the shorter hairs of group 58.

Jeswiet groups 51 and 52.—The upper or throat surface of the dewlaps bears two hair groups. In one group the hairs are short and of the type found on the lower surface; in the other, they are long and often cover up the shorter hair. The short hairs constituting group 52 either cover the entire surface of the dewlap (pl. 10, *E*) or are regionally restricted and prominent only along the outer marginal zone. Besides differences in regional distribution, there is much variation in length and denseness of hairs. In some varieties the hairs are very sparse; in others, they occur in prominent bands or form a uniform feltlike covering. The hairs are straight or curly and usually much appressed. The short hairs of this group are partly, sometimes entirely, covered over by a much longer pubescence consisting of silky lashes that continue to the outer edge of the dewlap. The hairs usually diminish in length toward the midrib. Within the group they are scattered or in strips. In some varieties, like Yellow Tip, group 51 is entirely wanting; in many others, especially those of the New Caledonia collection, it is restricted to a narrow marginal band; sometimes it covers one-half or less of the dewlap surface, and in some few varieties, the entire surface, even extending into the midrib. The hairs near the outer edge are always very long and project prominently over the margin. Some of the hairs grow directly on the edge and become continuous with the long and soft cilia of the basal part of the lamina (group 53). When group 51 is restricted to the marginal zone, it often forms a conspicuous tuft. In some varieties the prominence of the tuft is augmented by the presence of hairs on the tip and margin of the auricles.

LIGULE

General Morphology

The lamina is separated from the sheath by the ligule, a membranous appendage that contains no vascular tissue but is made up altogether of elongated parenchyma cells. In its young state it is translucent and hyaline; later it becomes dry, locally discolored, often brokenly indented and, in most wild cane varieties, torn.

As has already been pointed out for the dewlaps, the asymmetry of the lamina leaves its mark on the organs immediately associated with it. In the structure of the ligule, the asymmetrical condition reveals itself in the following departures from the bilateral design:

(1) One side of the ligule is usually wider than the other side, the degree of variation depending on the difference in width of the two sides of the leaf lamina.

(2) One side of the ligule is often less tall than the other side. This effect is produced by a rapid decrease in height of one side, while the other side retains its maximum height for some distance and then tapers gradually or abruptly as it approaches the edge.

(3) The two sides of the ligule often have a different steepness of slope (fig. 12, *E*), the side which corresponds to the overlying half of the sheath margin having a greater pitch than the other side.

Fundamentally there are four ligular patterns (fig. 12, *A–D*): Strap-shaped, deltoid, crescent-shaped, and bow-shaped.

The deltoid ligule (fig. 12, *B*) is found in many wild canes and is associated with the narrow type of leaf, especially with varieties where the lamina has been reduced to the width of the midrib. In this type of ligule, the height is about equal to the width at the base. In all other forms, the width at the base is many times the maximum height.

In the strap-shaped ligule (fig. 12, *A*), a relatively rare type (Raiatea 1, Imp. 923), the height remains practically unchanged. The crescent- and bow-shaped ligules are tallest in the middle, gradually or rapidly thinning out toward the margin of the leaf. In the crescent-shaped type, there are forms with a relatively high and convex central part and forms in which the upper free margin remains horizontal (pl. 10, *B*). In the bow-shaped type, the central part is depressed with the flanges either horizontal or sloping. The upper free edge of the ligule may be entire or notched. The latter condition is often restricted to the flanges near the margin of the leaf; however, the entire edge may be emarginate. The notched or emarginate condition of the ligule must not be confused with structural changes accompanying the aging of this organ as is observed especially in the deltoid type, which on maturity often becomes torn.

The middle part of the ligule, which overlies the midrib, varies in height between 2 and 8 mm. It shows the greatest variation in shape and generally is responsible for the many different and intergrading types. The upper margin of this region is flat, raised, or depressed, producing the broadly curved, pointed, or arcuate ligular effects. A depressed upper central region is always associated with the bow-shaped ligule (pl. 10, *D*), while curved sloping flanges and a horizontal central edge produce the subarcuate types.

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The lower margin of the ligule, which is inserted in the tissue of the leaf, also shows a variation in the shape of the central region. Crescent-shaped ligules with a broad- or round-pointed upper-central region may have a convex basal margin; in some, this region is obcordate, projecting downward rather than up.

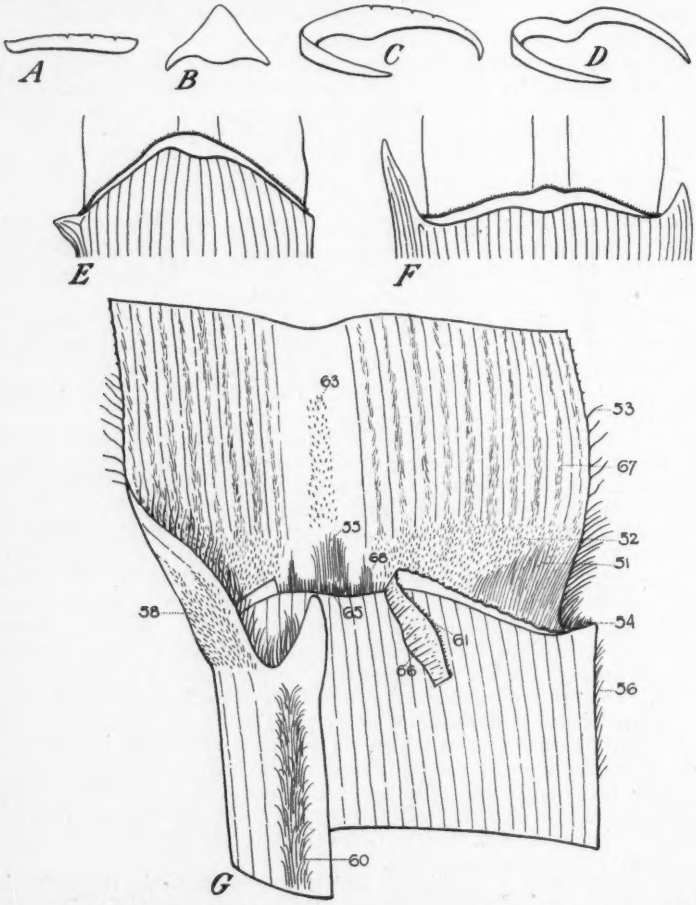

FIGURE 12.—Structure of different types of ligule: *A*, Strap-shaped; *B*, deltoid; *C*, crescent-shaped; *D*, bow-shaped; *E*, asymmetrical, steeply sloping ligule; *F*, asymmetrical horizontal ligule; *G*, detailed structure of blade joint, showing location of the various hair groups.

The two ends, or flanges, of the ligule normally terminate at the edge of the leaf. In some forms with transitional types of auricles, these flanges may project a short distance beyond the leaf edge; in others, they may be abnormally decurrent, running almost vertically downward before terminating (pl. 10, *F*).

Pubescence

The ligule is glabrous and shiny on the adaxial surface. The side next to the leaf is rarely smooth but is usually covered with partly free or completely adnate hairs (Jeswiet group 66). These dorsal hairs arise at the base of the ligule, remain adnate to the epidermis for a certain distance, become free near the apex, and often project some distance above the free margin of the ligule. In certain varieties like Striped Mauritius, the hairs of group 66 are adnate in the center of the ligule but completely free at the flanges and often several times the height of the ligule. Sometimes the dorsal hairs are very few in number; at other times they are dense and the surface may appear slightly ribbed wherever the hairs are completely adnate. In certain varieties the hairs are short; in others, they project quite far above the free margin of the ligule.

The upper margin of the ligule is almost invariably ciliate, although there is much variation in both density and length of these hairs. Sometimes the cilia are inconspicuous in the central part and prominent at the flanges. The hairs making up group 61 (pl. 10, *G*) are really of two types: those that are extensions of the apical epidermal cells and those that morphologically belong to group 66, being the free tips of hairs that originated near the base of the ligule but remained completely adnate, becoming free only a little distance below the upper margin.

Pubescence on Midrib

On the midrib behind the ligule, there are found, in certain varieties, a number of hair groups (figs. 12, *G*, and 13, *A–D*) which Jeswiet named groups 55, 63, 65, and 68. Not all of these groups are found on one and the same stalk, not even in one and the same variety; but a combination of two groups is not uncommon.

Group 55, according to Jeswiet (*15*), is very rare in *Saccharum spontaneum*, although he refers to it quite frequently in his description of varieties. It was observed by the writer in a number of canes from the New Caledonia and other collections. It is a fairly prominent group of rather long or medium-long hairs, forming a shallow tuft the width of the midrib or narrower. Associated with it, although often occurring independently, is group 63. This group forms a triangular or linear patch, from a few millimeters to several centimeters in length, usually inserted directly at the base of the ligule or, if group 55 is present, directly above this group. The hairs are always short and appressed, scattered or crowded, usually inserted obliquely, and visible to the naked eye because of their silvery sheen.

Group 65 differs from 55 in having the hairs arranged in a single row which does not project above the free margin of the ligule. According to Jeswiet (*15*), the row extends over the entire width of the leaf blade. But in his varietal descriptions (*15–24*) he limits it to the region of the midrib, a location which is in agreement with the data embodied in this paper. Group 65 appears to be closely associated with the dorsal pubescence of the ligule (fig. 13, *A*). In varieties in which the hairs of group 66 are long and free, one finds that, upon separation of the ligule from its place of attachment, some of the long hairs remain with the ligule while other hairs belonging to the same group are left behind as a fringe implanted in the tissue of the blade

(fig. 13, *A*). In varieties where group 55 is small and the hairs are short, it is easily mistaken for group 65. Another difficulty is encountered in canes where the long hairs of group 51 reach as far as the midrib; in such instances, it is impossible to trace group 65 beyond the confines of the midrib. This may have been the reason why Jeswiet in his descriptions limited the group to the midrib.

Of rare occurrence is Jeswiet's group 68—two pointed tufts of long or medium-long hairs implanted behind the ligule on the two

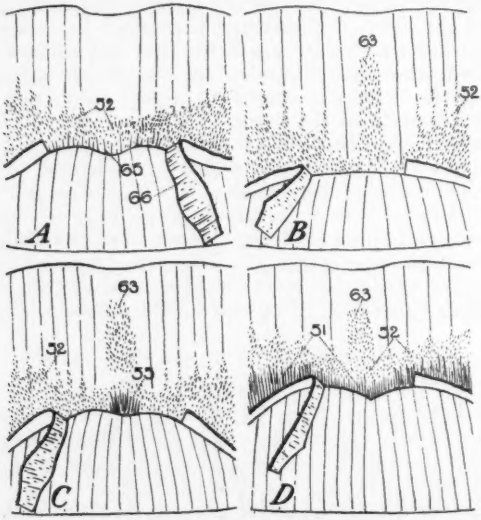

FIGURE 13.—Hair groups on midrib and their relation to the hairs of the dewlaps; the ligule is folded back to show insertion of hair groups. *A*, Group 52, extending across midrib; hairs of groups 65 and 66, similar in origin and appearance. *B*, Group 52, extending partly across midrib; group 63, attached to base of ligule. *C*, Group 52, extending across midrib; group 55, inconspicuous; group 63, fairly prominent but short. *D*, Hairs of groups 51 and 52, extending across midrib.

outer margins of the midrib and basally connected with group 65. This group has not been observed in the material studied by the writer.

Although groups 51 and 52 usually terminate at the midrib or some distance before reaching it, there are varieties, especially among the wild canes, in which either or both of these groups reach across the midrib, making the identification of the four midrib groups difficult or impossible.

AURICLES

General Morphology

The auricles are ear-shaped appendages of the leaf sheath. In sugarcane they form pointed structures that are asymmetrical, often weakly developed or altogether wanting. Auricles, if present, reach full development rather early in the ontogeny of the leaves; they are well developed, even on the youngest leaves, although

differing in shape from those on mature organs. As soon as the blade joint is exposed, the auricles begin to degenerate; they become dry and brown and often shrivel up, the change keeping pace with similar changes in the upper sheath margin, which, as we have seen earlier, becomes discolored and dry on maturing.

Jeswiet (*15*) recognizes four types of auricle development, which are briefly as follows:

(1) Canes with two well-developed auricles but with the inner one the larger.
(2) Canes in which only the inner auricle is well developed, while the outer one is a transitional structure.
(3) Both inner and outer auricles of the transitional type.
(4) Both auricles wanting and the leaf sheath merging imperceptibly with the blade.

This classification has been retained, but, for the sake of convenience, it was found advantageous to subdivide the first group into canes in which both auricles are well developed and canes in which the inner auricle is invariably larger than the outer.

A typical cane variety in which the auricles are altogether wanting is Hatooni; the sheath is of the same width as the blade and only a slight constriction in the dewlap region marks the transition.

Canes with the transitional type of auricle are very common. The blade passes into the sheath, either with a slight curve or rather abruptly under a right angle. The latter type is frequently found in Jeswiet's second class, where only the inner sheath margin has a well-developed auricle. When both auricles are of the transitional type, the outer one may be right-angled while the inner joins the blade under a slight curve. In some varieties, the reverse holds true.

The types with one or two well-developed auricles (fig. 12, *F*) are most common. A good example of the latter is Red Tip, which has two large auricles, both of approximately the same shape.

The auricles are inserted high or low, at the same level or at different levels. In horizontal ligules, the line of insertion of the two auricles lies in the same plane and, if the auricles are large, their tips may project prominently above the upper margin of the dewlaps. The insertion point of the auricle usually coincides with the termination of the ligule, but in many Hawaiian Originals, which have decidedly sloping ligules, the inner auricle is inserted at a considerable distance below the termination of the ligule (fig. 14, *C*).

The asymmetry of the auricles reveals itself both in the different size of the two organs and in their height of insertion. In forms with horizontal ligules, the auricles are inserted high; in forms with sloping, asymmetrical ligules, the inner auricle is inserted somewhat higher than the outer.

Although there is some variation in size and shape of the auricles on the same stalk, a pattern characteristic of the variety predominates. The most typical auricle shapes are illustrated in figure 14. Most common is the deltoid pattern, varying from the short and rather blunt to the lanceolate type. Auricles of the lanceolate type are very common and are found in almost any size. Less frequent are the falcate, calcariform, and unciform shapes.

PUBESCENCE

The free upper edge of the auricle is smooth or ciliate (Jeswiet group 54). The hairs often cover only part of the free edge, but

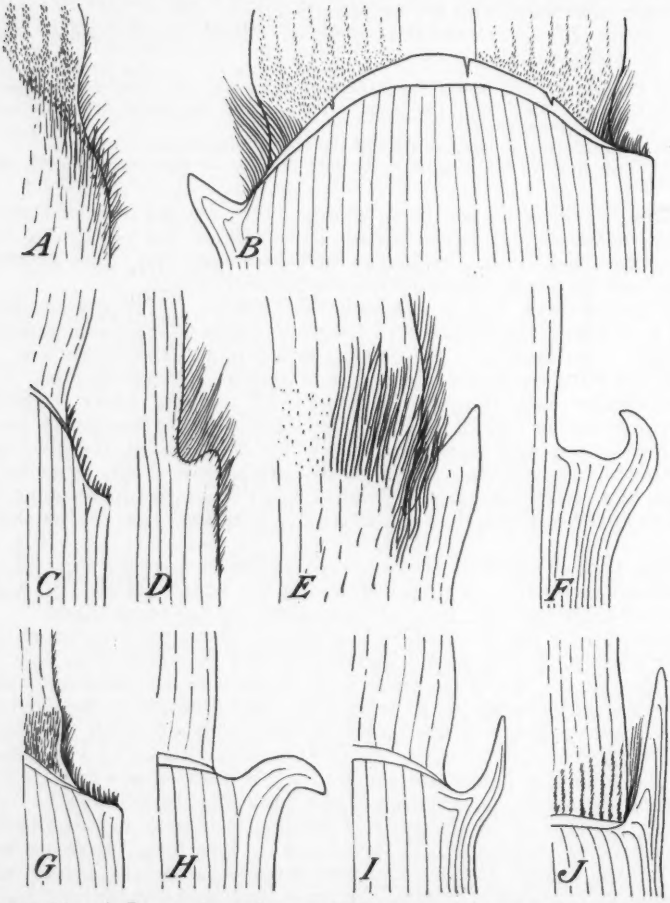

FIGURE 14.—*A*, Long spines of group 60 become confluent with group 54 and partly cover short pubescence of dewlap, 28 N. G. 49; *B*, outer auricle of transitional type, inner auricle deltoid and inserted lower than outer auricle, N. C. 53; *C*, low-inserted inner auricle, Hawaiian Original 36; *D*, hairs at overlying sheath margin (group 60 or 56) and hairs on tip surface of auricle (group 70) confluent with marginal cilia of auricle (group 54), Chunnee; *E*, hairs of group 60 partly cover outer surface of dewlap, N. C. 11; *F*, unciform type of auricle; *G*, transitional type of auricle; *H*, calcariform type of auricle; *I*, falcate type of auricle; *J*, lanceolate type of auricle.

in some instances they extend to the very tip (pl. 10, *A*) or even descend down the outer margin (pl. 10, *C*). In the transitional type of auricle, where the sheath changes into the blade under a right or an obtuse angle, the edge may be ciliate up to the sheath

margin and, if group 56 is also present, the cilia of the two groups may appear continuous with one another.

In a few varieties, the surface of the auricles is covered with long hairs, mostly along the outer margin. When occurring on the inner auricle, the group is known as 71; when on the outer auricle, as group 70. Jeswiet (*20*) reports them principally for Chunnee crosses. In varieties with strongly developed lateral patches (group 60), hairs of these groups may become continuous with those of the auricles. When the surface of the auricles appears glabrous, the epidermis under the microscope shows nevertheless numerous short spines, which take the place of silica cells in the typical short group.

STABILITY OF CHARACTERS

The less variable a character, the more useful it is in the general classification scheme and in delimiting a variety.

Characters may differ qualitatively and in degree, representing the expression of inherited tendencies modified by environment. Some of the changes take place during the normal course of development; others are speeded up or retarded by abnormal external conditions. Excessive variability may be due to an unbalanced hereditary make-up.

Certain characters, such as pubescence and structure of epidermis, are fixed during early development; others change progressively, attaining full expression at the culmination of vegetative growth, with some modifications even after the advent of maturity. Frequently retrogressive changes set in, resulting in death or the loss of an organ.

Hair groups and epidermal structure are largely fixed characters that can be studied satisfactorily in young plants though some hair groups become more prominent late in ontogeny. Qualitative variations, such as the occasional absence of certain hair groups or their unilateral distribution in some of the buds on a stalk, are quite common; they are apparent very early and may not change in character as the plant continues development. Certain hair groups, like group 58 on the outer side of the dewlaps, are most conspicuous when young, since secondary changes, e. g., the deposition and subsequent discoloration of wax on the dewlaps, are apt to mask the hairs, making evaluation of the group difficult. The epidermis, on the other hand, is best studied in mature material, not because of any change in the epidermal pattern but because of the greater ease of handling mature tissue in preparing it for microscopic examination.

The great majority of characters are modified in one way or another during vegetative growth. Usually only certain aspects of a character are changed while others remain stable. An instance is the ligule, which shows a characteristic type pattern even in very young leaves. Changes concomitant with further development may involve only an increase in slope in varieties that are characterized by a steeply sloping basal region.

During ontogeny, organs not only enlarge but also change in shape. The change may be superficial or pronounced, but almost always there is a distinct resemblance between the juvenile and the mature form.

Practically all internodes are cylindrical when young but assume a characteristic form pattern at or somewhat before maturity. Abnormal environment such as prolonged dry spells may cause, according to

Jeswiet (*15*), cylindrical internodes to become conical and tumescent internodes to become cylindrical, while other factors are responsible for the appearance of short, tumescent forms. Associated with the development of certain internode patterns is the shape of the root band; obconoidal internodes are joined to conoidal root bands, and internodes shouldered at the base opposite the bud have an obconoidal sector in the corresponding region of the root band. Changes in the growth ring during development are limited. The young growth ring is usually flush with the internode or somewhat depressed; later it may bulge as a narrow ring on the bud side or around the entire circumference. Changes in shape of dewlaps are in the beginning associated with changes in the slope of the ligule and later with a change in leaf carriage. Young dewlaps are often narrow, with a more or less horizontal basal margin. Some retain this form during subsequent growth; others may change this strap-shaped juvenile form to a more characteristic deltoid or squarish type. Often the change is more apparent than real, since an unmistakable type pattern persists during growth.

The situation is somewhat different in auricles that are advanced in development, even in young leaves. They are apt to retain their juvenile form if it is of the conventional deltoid or lanceolate type, but change if of a more unusual design, viz, unciform, calcariform, or falcate. Auricles of the transitional type are alike in young and mature leaves.

Buds usually enlarge uniformly during ontogeny; they may lose their flatness but retain a fundamental design characteristic of the variety.

Color changes affect all parts of the plant that are protected when young and become exposed in the course of development. Often there is merely a darkening or intensification of the color; at other times, the change is more radical, as in certain dewlaps that are bright red when young and brownish olive when mature. Growth ring and root band are at first a pale green or ivory; they change gradually until they are approximately concolorous with the internode. Sheath and leaf blade often become a darker green, and the purplish tinge that characterizes the young state in some varieties is absent from the mature organs.

In a normal environment, these color changes follow a given sequence, so that the color of a cane during vegetative growth is rather typical of a variety. If exposure to light is gradual, the color variations, especially in the stem, are not nearly so pronounced as when the change is abrupt; for this reason a cane from the middle of a field has stalks colored differently from canes at the edge of a planting. The quality of light influences color. This is noticeable in greenhouse specimens, which frequently differ in stem color from a plant of the same variety grown outside. Higher altitude with accompanying lowering of temperature has, according to Jeswiet, also a marked effect on pigmentation, so that the color of a variety growing in the plains differs from that grown at higher elevations.

Sunlight not only affects the color of a stem but may further alter the stem surface by inducing formation of corky cracks or by intensifying their development. Often the color is modified by the presence of wax, with additional changes induced by the growth of molds that

may give the effect of a sooty discoloration. Other changes are effected by the sloughing off of the waxy layer in stripes or irregular patches. Hairs and wax, separately or in combination, often affect the color of the dewlaps. In young organs the felty pubescence often produces a silvery sheen, masking the original pigmentation; later in ontogeny, heavy layers of wax may be deposited, which, on discoloration, give the dewlaps a dirty-olive or blackish tinge, regardless of the original color.

Certain changes of form are coincident with the development of neighboring organs. An instance is the dewlaps, which often have to adapt themselves to a changed leaf carriage. When the leaves change from an erect to an ascending habit the dewlaps compensate at first by enlargement whereby the length of the outer dewlap margin is increased, later by passive stretching, a process facilitated in leaves that have conspicuous folds in the dewlaps. Eventually the dewlaps become torn, especially during unfavorable, stormy weather. Other organs merely enlarge after maturity. Thus flat buds may become plump, bend away from the stalk, and elongate; root primordia swell and develop into rootlets. All these changes represent tendencies that are normal in some varieties but are induced in others by changes in environment favorable for their expression.

Quite common are certain retrogressive changes that may set in even before the advent of maturity. The upper membranous margin on the leaf sheath and also the auricles begin to wither and turn brown before growth is complete. Similar changes take place in the sheath-base region. This part of the leaf sheath, which first acts as an intercalary meristem during active elongation, becomes the zone of abscission when the leaves are shed. If the leaves are retained, the sheath base darkens and shrivels somewhat. The ligule loses its transparency, the margin develops cracks, the texture becomes leathery, and the color an uneven brown. The dewlaps, as already stated, are similarly affected; they become discolored and torn, often long before the leaves are shed. The membranous margin and basal appendage of the prophyllum wither and become discolored while active growth may still be in progress; eventually the entire prophyllum turns an uneven brown. While certain of its hair groups, especially on the wing, tend to become more prominent, those on the side of the prophyllum grow less conspicuous so that old buds have a striking, polished appearance.

Stability of vegetative characters is only relative, for what appears more or less fixed in one variety shows much fluctuation in another; this applies to both qualitative and quantitative characters. For example: Hair group 11, on the anterior side of the prophyllum, may be found on all buds of a stalk or stool and be equally prominent on both halves of the anterior side; in another variety, the group may be limited to a certain number of buds; in a third, the group may show further reduction by being occasionally absent from one or the other half of the anterior side. It goes without saying that hair group 11 has a greater diagnostic value in canes of the first group than of the other two. Other characters may show even less dependability. A normal environment may intensify normal variations or have little or no effect on them. Characters that vary little are usually associated with conservative organs. A structure of ancient origin, without much tendency to variation and not subject to modification under the influ-

ence of environment, is the ligule, as shown by Panje (*29*) in his study of *Saccharum spontaneum*. The stem epidermis is another structure that is especially useful in tracing out taxonomic relationships.

The proper evaluation of hair groups from the standpoint of their taxonomic usefulness is at best an unsatisfactory undertaking. A glance through Jeswiet's and the author's varietal descriptions shows that only a certain number of hair groups, rarely more than 50 percent, are constant and these include the more common groups; the ones most suitable for diagnostic purposes are often absent and their distribution is usually erratic. It is of little comfort to have on the check list such groups as groups 1, 12, 21, and 26, since their occurrence is almost universal on sugarcane buds; only quantitative and, to a certain extent, qualitative differences within group limits, if constant, give these groups a certain value. Often the mass effect produced by the bud pubescence in general is more important for rapid diagnosis than is a study of the individual groups. Occasionally, certain solitary groups are so prominently developed that their presence suffices to delimit a variety.

The hair groups on blade and leaf sheath are often more reliable and more easily evaluated than those on the bud. Their utilization in descriptive work involves qualitative as well as quantitative differences. Group 57, for example, is either present or wanting but, when present, may vary in distribution so much that it loses its value as a quantitative character. Group 60 occurs relatively seldom and is proportionately more valuable than the dorsal patch. The marginal fringe of the ligule is very useful in extreme cases (e. g., Kassoer, with a very tall marginal fringe, compared to Shamsara, where these hairs are extremely short). On the other hand, the hairs on the midrib back of the ligule often show too much variation to be really dependable, although in certain varieties (N. C. 11, 29, and 78) some of these groups (63 or 55) are rather constant. The hairs on sheath joint and decurrent sheath margin are of importance in certain taxonomic groups. Group 59 is very variable, occurring over the entire circumference of the sheath joint or in localized regions; often a certain regional distribution of hairs is so constant as to constitute a character within a character, making it seem advisable to break up this group into smaller units.

The velvety pubescence of the blade (group 67) is very striking and represents one of the most clear-cut characters. It is not so rare as suggested by Jeswiet and should be of value in any classification scheme.

The microscopic pubescence of leaf blade and sheath, in fact the structure of the epidermis of these organs in general, is often important in differentiating varieties when tracing relationships. For example, stomatal grooves are found on many but not all wild canes, and the giant solitary spines occur on the leaf lamina of only a few of these varieties.

Occasionally certain characters are so limited in their distribution as to have been recorded only once or twice in literature. An example of such a character is the hairiness of the stalk of New Caledonia 32 and 75 Lehu of the collection recently studied by the author.

SUMMARY

Sugarcane is a tall perennial grass with the culms bunched in stools or evenly scattered, erect, ascending, or prostrate. The internodes are alined or staggered and attain their characteristic development—form, length, diameter, and shape of cross section—in the middle part of the stalk; dwarfed and abnormally long internodes may occur. The surface of older internodes is often marked by corky cracks or growth cracks, and there may be a more or less conspicuous bud furrow present. The stalks are covered with a layer of wax of varying thickness that forms a distinct band at the top of each internode. The color of the stalk varies in young and milling cane, and it may be modified by external factors and by the action of surface mold on the wax deposit.

The internal tissue of the stalk has a uniform color, or the center may differ by being whitish and pithy; often there is a distinct cavity in the center. The vascular bundles of the peripheral ring are few or relatively numerous, uniformly small or varying in size; their sheaths, discrete or confluent. The structure of the stem epidermis is influenced by the absence of silica cells, the predominance of pointed cork cells, and other minor factors.

The node contains root band and growth ring. The latter may be wide or narrow, flush with the internode, constricted, or bulging. The root band may be high or narrow; of even height or taller on the bud side than on the opposite side; cylindrical, conoidal, or obconoidal. It contains one or several rows of root primordia, which are widely spaced or crowded, oval or round, dormant or with a tendency to sprout in the field.

The buds are placed alternately, each node bearing normally a single bud. They are inserted directly above the sheath scar, sometimes slightly lower or appreciably higher. The tip may or may not reach the growth ring but quite often projects some distance beyond. In some varieties, the buds are flush with the stalk or even depressed; in others, protruding. Color varies with variety and with age; often there is a contrasting coloration between side and wing tip in young buds. Buds may be large or small, short or long, flat or cushioned; their shape may be oval, ovate, obovate, pentagonal, rhomboid, triangular, or round.

The visible part of the bud is the prophyllum. It forms in its entirety an asymmetrical hood with the large front side composed of two overlapping halves and the short posterior side entire. The prophyllum consists of sides and wing; both show much variation in form and together determine the bud pattern. The edge of the overlapping half of the anterior side of the prophyllum forms a membranous margin that may terminate in an appendage. Other appendages may occur along the membranous margin, at times covering the germ pore or enlarging to form the beaked or rostellate bud forms. The wing of the bud may be inserted at, above, or below the center of the prophyllum; it may be wide or narrow, sometimes wider at the base than at the apex. The corners of the wing may be auriculate, the edges entire or emarginate. The tip of the bud is variously pointed, its margin smooth or notched. The venation of the prophyllum is

prominent or obscure, the veins straight or radially converging, the germ pore apical or central. The prophyllum may be practically smooth or pubescent, with the hairs arranged in more or less definite, distinct, or confluent groups; their occurrence and constancy are considered valuable taxonomic characters.

The leaves are two-ranked and consist of sheath and blade. At the juncture of sheath and blade is the blade joint with its specialized regions and at the base of the sheath is the leaf sheath node or sheath base.

The blade is erect, ascending, and gently curved, or erect with drooping tip. The surface is leathery, smooth, or rough; the veins conspicuous or faint. The midrib is either broad and massive or more or less shallow. The blade is relatively wide or narrow, sometimes reduced to the width of the midrib at the base. The edges are usually scabrous, the surface smooth except for microscopic hairs or a soft velvety pubescence. The upper and lower epidermis have each a characteristic pattern, varieties differing as to the presence of spines, stomatal grooves, and width of bulliform bands. The color of the blade is a shade of green, sometimes with a purplish cast.

The sheath forms an open tube, with the outer margin overlapping the inner. The outer margin is drawn out into a membranous border, which is often decurrent at the base and even appendaged. The leaves become abscissed at the sheath base, leaving a characteristic scar that may be prominent or inconspicuous, straight or oblique, sometimes spreading and sagging under the bud. Sheath length is more or less constant within varietal limits. The surface is usually waxed and often covered with a vestiture of hair regionally distributed in definite groups. Characteristic hair groups are also found along the upper and lower decurrent sheath margin and at the base of the sheath joint. The epidermis shows broad intercostal regions and specialized zones overlying the veins. Varietal differences, based on the presence of spines and other characters, are valuable in classification.

The dewlaps, or joint triangles, are large or small, broad or very narrow, deltoid, squarish, or ligular. They are often asymmetrical. Their color differs considerably in young and mature organs and is subsequently altered by discolored wax deposits on the outer surface. Typical hair groups are present on both outer and inner surfaces. The ligule, a membranous appendage that separates the sheath from the blade, may be deltoid, strap-shaped, crescentiform, or arcuate, of uniform or asymmetrical construction; the free edge is often prominently ciliate and the back scabrous with free or partly adnate hairs. Back of the ligule, on the midrib, are a number of small hair groups constituting important taxonomic characters. Often there are present auricles, ear-shaped appendages of the sheath. In many varieties they are entirely wanting, in others they form transition structures; usually they are well developed, the inner almost always more prominently than the outer. There are many different morphological forms with variation in size within the different groups. The free edge of the auricle is usually ciliate, and the outer surface may, on rare occasions, bear tufts of long hair.

Characters differ qualitatively and in degree, and their stability is only relative. They represent the expression of inherited tendencies modified by environment. Characters that vary little are

usually associated with organs of ancient origin such as the ligule. The hair groups established by Jeswiet have a definite place in the classification scheme, but their value is only relative.

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STIGMA RECEPTIVITY AND POLLEN SHEDDING IN SOME PECAN VARIETIES [1]

By C. L. SMITH, *physiologist*, and L. D. ROMBERG, *assistant horticulturist, Division of Fruit and Vegetable Crops and Diseases, Bureau of Plant Industry, United States Department of Agriculture*

INTRODUCTION

The pecan (*Carya pecan* (Marsh.) Engl. and Graebn.) is a monoecious tree in which pollination is effected by the wind. The catkins, which bear the staminate flowers, arise from lateral, axillary, composite buds situated on the previous season's growth. These buds are formed as the shoot is produced, and the catkin primordia are differentiated at the time of bud formation when the subtending leaves are about one-tenth grown.[2] The catkin primordia occur on the sides of a central vegetative growing point within the composite group. The pistillate flowers are differentiated during the last of February and the first of March within terminal or lateral buds borne on shoots of the previous season.[3] The pistillate flowers make their appearance soon after shoot elongation begins in the spring. Normal bearing trees may develop catkins from practically every node, but shoots that bear pistillate flowers are usually produced only from buds located at or near the terminals of the shoots.

The possibility that failure of self-pollination might result because of maturity and shedding of pollen either before or after the stigmas of the pistillate flowers are receptive was first investigated by Stuckey,[4] who concluded that varieties of the pecan may be divided into two groups with respect to the time of pollen shedding and stigma receptivity. In one group, characterized by short, thick, compact catkins, he reported that pollen generally matured at about the time the stigmas became receptive; in the other group, characterized by relatively long, narrow, and less compact catkins, the stigmas became receptive 2 to 10 days before the staminate flowers shed their pollen. In this case a large percentage of the stigmas became dried or callused before the pollen was shed. However, Stuckey also stated that—

> the difficulty in drawing definite conclusions * * * lies in the fact that in making field observations it is very difficult to determine just when the stigmas of pecans become receptive and the exact time when they pass the receptive stage.

Woodroof [5] gave dates of pollen shedding and of stigma receptivity for 4 years and indicated that some varieties are not capable of self-pollination in most seasons. He stated that the normal period of receptivity of a single stigma is about 5 days but that the length of the receptive period is very responsive to conditions of temperature and humidity. He concluded that pollen is shed immediately upon

[1] Received for publication October 9, 1939.

[2] WOODROOF, J. G. STUDIES OF THE STAMINATE INFLORESCENCE AND POLLEN OF HICORIA PECAN. Jour. Agr. Res., 40: 1059–1104 illus. 1930.

[3] ——— and WOODROOF, NAOMI CHAPMAN. FRUIT-BUD DIFFERENTIATION AND SUBSEQUENT DEVELOPMENT OF THE FLOWERS IN THE HICORIA PECAN. Jour. Agr. Res. 33: 677–685, illus. 1926.

[4] STUCKEY, H. P. THE TWO GROUPS OF VARIETIES OF THE HICORIA PECAN AND THEIR RELATION TO SELF-STERILITY. Ga. Expt. Sta. Bul., 124, pp. [127]–148, illus. 1916.

[5] See footnote 2.

maturity of a catkin if conditions are suitable, but not if the temperature is too low or the atmospheric humidity above 85 percent.

Adriance [6] gave the range of maturity of staminate and pistillate flowers for 6 years at College Station, Tex., and concluded that "the type of dichogamy in the pecan is not always fixed * * * there is a very strong tendency in certain seasons toward protandry and in others toward protogyny." On the basis of his data the varieties were classified into three groups: Protandrous, fluctuating, and protogynous. The shift in dichogamy was attributed to differences in response to varying weather conditions in late winter and early spring. He stated that "moisture and high temperature during the spring season favor early maturity of the staminate flowers, and cool, dry seasons favor the earlier maturity of the pistillate flowers."

Since definite knowledge of the dichogamy of varieties is necessary to insure adequate pollination in the pecan orchard, experiments were initiated to determine the periods of stigma receptivity by controlled pollination and the set of nuts. Previous workers determined the period of receptivity of pecan varieties by observation of the stigmas during their development. This method was not considered entirely reliable, because of the probability that pollination would alter the condition of the stigmas, and, as stated by Stuckey,[7] it is extremely difficult to judge receptivity near the beginning or end of the period.

EXPERIMENTAL METHODS

In order to carry out the experiments under conditions of controlled pollination, it was necessary to cover the pistillate clusters to prevent wind-blown pollen from coming into contact with the stigmas. Traub and Romberg [8] used small paraffined cloth bags as flower covers; but such bags were not entirely satisfactory, since they were relatively heavy, shaded the flowers, and held moisture to such an extent as to subject the pistillate clusters to an abnormally high humidity. It is not known how these conditions affect stigma receptivity. Therefore, in the work reported herein, bags made from viscose sausage casings were used. These were light in weight, transparent, and permitted diffusion of gases and water through them. In comparative tests these bags proved to be superior to the cloth bags in every respect. The size of bag found to be most satisfactory was 1⅛ by 4½ inches.

The bags were placed over the pistillate clusters before the stigmas were receptive and were tied securely upon a band of cotton placed around the tender young shoot for padding (fig. 1, *A*). Most of the small leaves near the base of the pistillate cluster were pinched off to facilitate covering. After these leaves are pinched off, the remaining leaves are stimulated into rapid growth and growth of other leaf and shoot buds is initiated. If the leaves or new shoots are allowed to develop to any appreciable extent in the bags, the pistillate clusters will abscise. Therefore, it is necessary to visit the bagged clusters once a week and pinch off the new leaves and shoot buds, which can be done without removing the bags.

[6] ADRIANCE, GUY W. FACTORS INFLUENCING FRUIT SETTING IN THE PECAN. Bot. Gaz. 91: 144-166, illus. 1931.

[7] See footnote 4.

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Whenever possible, 4 trees and 100 clusters per tree were used for each variety. An experienced man was able to put on approximately 400 bags per day.

Pollinations were made by means of a hypodermic needle and syringe without removing the bags, the needle being inserted through the cotton pad. The syringe consisted of a rubber bulb, of the type used to water automobile batteries, and a one-hole stopper into which was inserted a glass tube (fig. 1, *B*). A 20-gage hypodermic needle 1½ inches long was attached to the glass tube by means of rubber tubing. A loop in the glass tube was used to control the quantity of pollen applied per cluster. Numbered tags were attached to the shoots at the time of pollination to identify the clusters. The pollen was collected as follows. Mature catkins were picked and spread on

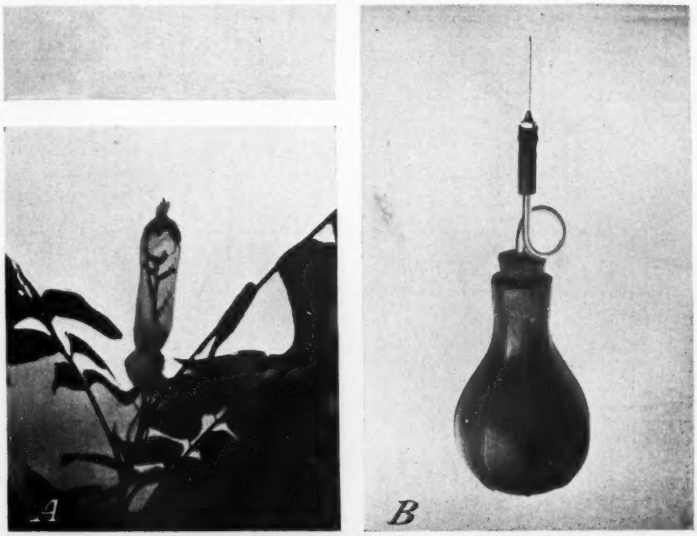

FIGURE 1.—*A*, Viscose bag for controlling pollination; inside the bag a leaf is growing, which if not pinched off might cause abscission of the pistillate cluster. *B*, Syringe used in pollinating bagged pecan flowers.

paper to dry. After 12 to 36 hours, the liberated pollen was collected and passed through cheesecloth or a fine-mesh sieve to remove foreign matter. The pollen was then placed in the rubber bulb of the syringe if it was to be used immediately. When it was to be used after 1 or more days it was spread in a thin layer in a covered cardboard box for storage. Thus kept, it was found to remain viable for not less than 7 days. Usually some old pollen was added to freshly sieved pollen in order to give greater bulk.

Pollination was commenced just before the beginning of stigma receptivity, as nearly as possible. On an average, about 16 clusters of each variety were pollinated each day during the period of receptivity. Random samples of nut clusters were obtained by pollinating them in the order of their occurrence in rotation about the trees.

Some clusters were left unpollinated to serve as checks on the degree of pollination control obtained and to indicate the time of dropping of unfertilized nuts.

As soon as the stigmatic surfaces had dried, indicating that receptivity had passed, the bags were removed and a record was taken of the number of nuts per cluster. A second count of the nuts in each cluster was made in late June or early July, which allowed sufficient time for the unfertilized nuts to drop. The nuts remaining at this time were taken as the set. From the data of the two counts the percentage of clusters setting nuts and the percentage of nuts set

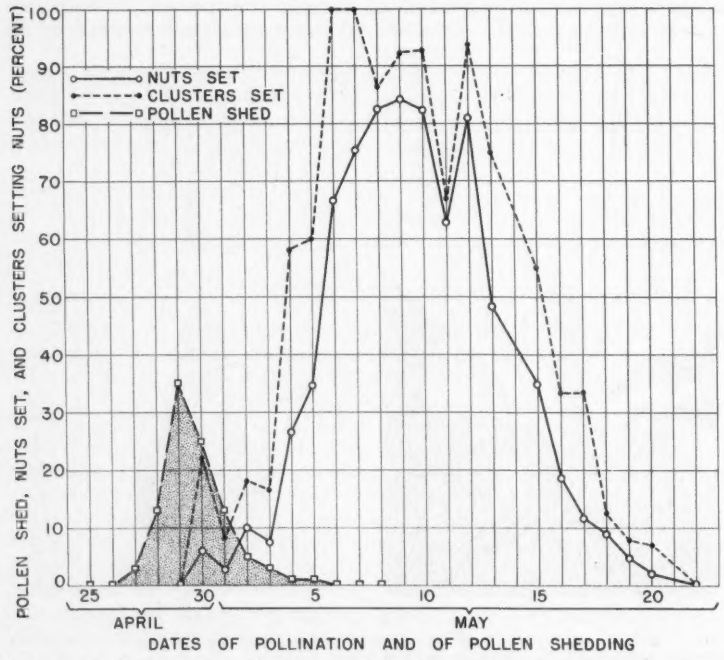

FIGURE 2.—Percentage of nuts set and of clusters setting nuts from controlled pollinations, and percentage of pollen shed on different dates during the season of 1933 by the San Saba Improved variety at Denison, Tex.

were calculated. In 1933 and in 1934, a larger number of clusters were left unpollinated and frequent counts of the nuts were made to determine more exactly the time that the unfertilized nuts dropped.

Owing to the relatively large size of the catkins, which ranged from 2½ to 6 inches in average length, it was easy to see the anthers, or portions of them, that had opened and liberated pollen. The amount of pollen that had been shed, expressed in percentage of the total on the tree, could be estimated. Such estimates were made daily for each tree. It is not presumed that these estimates are accurate; but this is the only simple quantitative measure that has been devised, and it is believed that it is a basis for better judgment of the polli-

nating possibilities of a variety than mere dates of first and last pollen shedding.

In 1933 the work was carried on in the Kemper orchard at Denison, Tex.; in 1934, at Austin; and in 1935, at Rogers. The Burkett, Sovereign (syn., Texas Prolific), and Schley varieties were used in each of the 3 years; Squirrel (syn., Squirrels Delight), Western (syn., Western Schley), San Saba Improved, Clark, Success, and Delmas, 2 years; and Stuart, Moneymaker, Kincaid, Jersey, Williamson, Halbert, and Onliwon, 1 year.

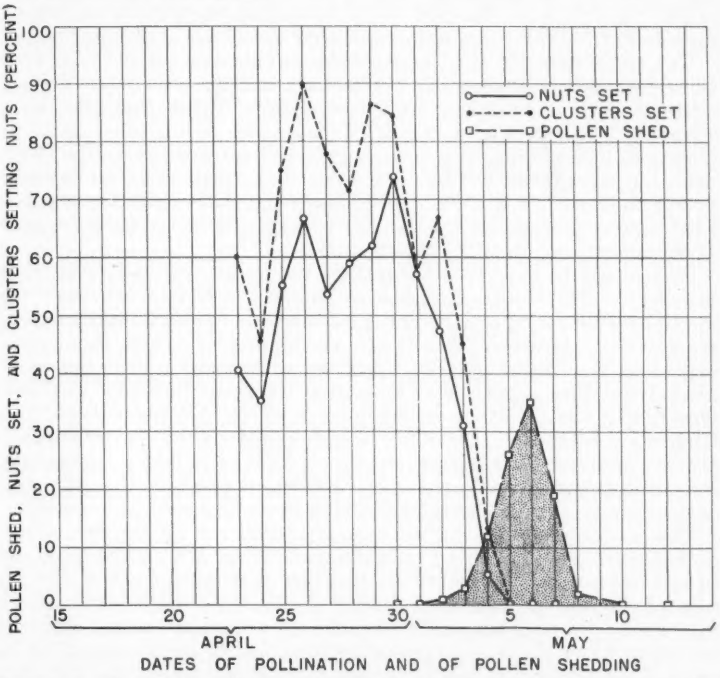

FIGURE 3.—Percentage of nuts set and of clusters setting nuts from controlled pollinations, and percentage of pollen shed on different dates during the season of 1934 by the Burkett variety at Austin, Tex.

In a study of dichogamy, made in 1935, the above-mentioned varieties were used and, in addition, the 11 following varieties: Humble, Bowers, Elgin, Russell, Odom, James, Teche, Alexander, Mosty, Mahan, and Curtis.

EXPERIMENTAL RESULTS

STIGMA RECEPTIVITY

Space does not permit the presentation of the detailed data obtained in the stigma-receptivity experiments during the three seasons. However, typical data for the percentage of nuts set and for the percentage of clusters setting nuts for each date of pollination are given in figures 2 and 3.

Clusters of San Saba Improved flowers were pollinated daily from April 29 to May 22 with the exception of May 14 and 21 (fig. 2). Beginning on May 1 and continuing for a period of 6 days, there was a rapid increase in the percentage of nuts set. This was followed by a period of 5 days during which a relatively high set of nuts was obtained, after which the percentage of nuts set decreased rapidly until May 17 and then more gradually to the end of the period. The total length of the stigma-receptivity period was 21 or 22 days. During the 7-day period from May 6 to 12, inclusive, the set of nuts might possibly have reached 100 percent had there been no losses of nuts from insect damage or causes other than lack of pollination.

The curve representing the percentage of clusters setting nuts shows the relationship between the clusters set and the nuts set. The percentage of clusters setting nuts was always higher than the corresponding percentage of nuts set. This was to be expected, since the setting of a single nut in a cluster gave 100-percent set on the cluster basis but usually much less on the nut basis, depending on the number of nuts in the cluster. In general, the data for other varieties were similar to those for the San Saba Improved except for the lengths of the receptive periods of the stigmas.

The pistillate flowers were not always pollinated early enough to include the first dates of stigma receptivity, and in a few cases pollinations were not made late enough to include the last dates of stigma receptivity. However, this is not considered of much importance, since near the beginning and end of the period only a few stigmas are receptive. The important dates within the range of receptivity of all flowers of a variety are those when a relatively high percentage of the flowers are receptive; therefore the approximate time during which 50 percent or more of the stigmas were receptive, as indicated by the set of nuts, was arbitrarily selected as the important period within the range of receptivity and will be referred to as the major receptive period.

The major receptive periods were determined by the set of nuts obtained in the day-to-day pollinations. Since it was apparent that causes other than the lack of fertilization prevented a set of 100 percent of the flowers pollinated during the period of high set, except in rare cases, 50 percent of the stigmas of a variety were considered receptive when the percentage set of nuts was at least one-half of the average set during the period of high set. For example, the San Saba Improved variety (fig. 2) set an average of 78 percent of the nuts pollinated from May 7 to 12, the period of high set. Thus the period from the 39-percent point on the upward slope to the 39-percent point on the downward slope of the receptivity curve represents the major receptive period of the stigmas, and extends in this case from May 5 to about May 14, or 9 days. This method could not be followed exactly in all cases, owing to fluctuations or incomplete data, and it was then necessary to make estimates. The major receptive periods, together with the first and last determined dates of stigma receptivity for the varieties used in this experiment, are given in table 1, and the major receptive periods are shown graphically in figure 4.

In most cases the length of the major receptive period varied from season to season in the same variety and in different varieties in the same season. The shortest period was 8 days for Stuart and Success

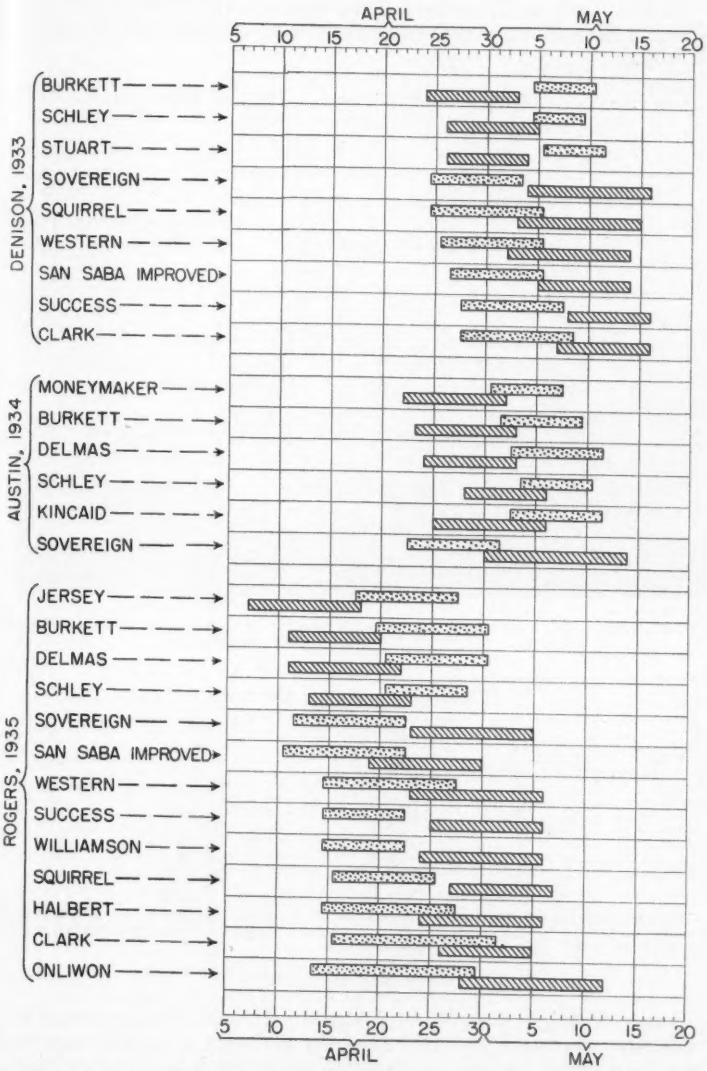

FIGURE 4.—Major periods of stigma receptivity and of pollen shedding in some varieties of the pecan, Texas, 1933–35. Dotted rectangles represent pollen shedding; cross-hatched rectangles represent stigma receptivity.

in 1933 and for Schley in 1934; the longest period was 14 days for Sovereign in 1934 and for Onliwon in 1935.

Studies made on 12 varieties showed that a period of 5½ to 6½ weeks after the date of last receptivity was required for all unfertilized nuts to drop.

TABLE 1.—*Time and duration of stigma receptivity of pecan flowers of several varieties during 3 seasons*

DENISON, 1933

Variety	Date of first stigma receptivity	Date of last stigma receptivity	Dates of major period of stigma receptivity [1]	Length of major period of stigma receptivity
				Days
Burkett		May 4	Apr. 24–May 3	9
Schley	Apr. 24	May 7	Apr. 26–May 5	9
Stuart			Apr. 26–May 4	8
Sovereign	Apr. 30	May 17	May 4–16	12
Squirrel		do	May 3–15	12
Western	Apr. 30	do	May 2–14	12
San Saba Improved	do	May 20	May 5–14	9
Success	do	May 18	May 8–16	8
Clark	May 4	May 22	May 7–16	9

AUSTIN, 1934

Moneymaker		May 3	Apr. 22–May 2	10
Burkett		May 4	Apr. 23–May 3	10
Delmas		May 8	Apr. 24–May 3	9
Schley		May 7	Apr. 28–May 6	8
Kincaid			Apr. 25–May 6	11
Sovereign		May 17	Apr. 30–May 14	14

ROGERS, 1935

Jersey		Apr. 22	Apr. 7–18	11
Burkett		do	Apr. 11–20	9
Delmas		Apr. 27	Apr. 11–22	11
Schley		Apr. 26	Apr. 13–23	10
Sovereign	Apr. 22	May 8	Apr. 23–May 5	12
San Saba Improved		May 6	Apr. 19–30	11
Western	Apr. 19	May 12	Apr. 23–May 6	13
Success	Apr. 21	May 9	Apr. 25–May 6	11
Williamson	Apr. 23	May 10	Apr. 24–May 6	12
Squirrel	Apr. 24	May 11	Apr. 27–May 7	10
Halbert		May 10	Apr. 24–May 6	12
Clark	Apr. 24	do	Apr. 26–May 5	9
Onliwon	Apr. 26	May 16	Apr. 28–May 12	14

[1] The major period of stigma receptivity is the period during which the daily set of nuts was 50 percent or more of the average daily set during the period of high set. This period extends from the first to the last date given and is not inclusive of both dates.

POLLEN SHEDDING

Pollen shedding normally begins gradually and ends somewhat more gradually, whereas in the middle of the period it is usually very rapid (figs. 2 and 3). In general, the earliest pollen is shed by catkins on a few branches somewhat low down and toward the inside of the tree, which are especially early in commencing growth in the spring (fig. 5). The last catkins to shed pollen are those on water sprouts growing on the trunk or large limbs of the tree or those on vigorous long shoots of the previous season, which start growth late and generally

are found on the outside and toward the top of the tree. The extent to which catkin development on a tree may vary is shown in figure 6.

FIGURE 5.—Young pecan tree at the beginning of growth in the spring, showing the extremes of variation in shoot development.

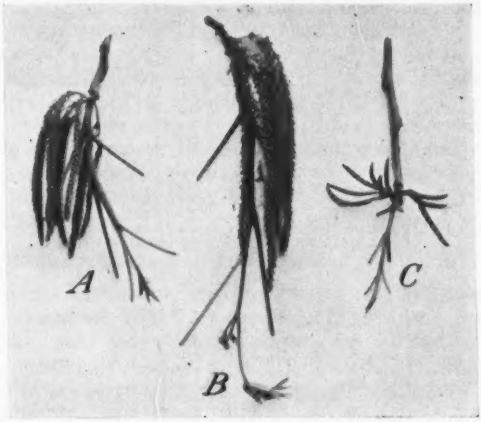

FIGURE 6.—Branches selected from a pecan tree on the same date, showing the extremes sometimes found in development of catkins and pistillate clusters and also showing the correlation in development of staminate and pistillate flowers originating from the same compound bud: *A*, Average; *B*, early; *C*, late.

It requires close observation to determine when pollen is first liberated and when shedding is complete. Therefore, the dates given as the first and last dates of shedding depend considerably upon the observer. It is often difficult to set any particular day as the last, owing to the presence of weak, poorly developed catkins, some of which may mature pollen still later. Also, a few pollen grains that have been retained or lodged in the catkins continue to be released. There is a strong tendency to disregard these small quantities.

In these experiments an effort was made to observe the very first and the very last pollen to be shed. Estimates also were made of the time interval from the date at which 1 percent of all pollen had been shed to the date at which 99 percent had been shed by each variety; this period, inclusive of both dates, will be referred to as the major pollen-shedding period. Under average orchard conditions it is doubtful if the first 1 percent or the last 1 percent of pollen is shed daily in sufficient quantities to effect a good set of nuts, whereas, in the interval between the time when 1 percent and 99 percent has been shed, the quantity shed daily should be sufficient to pollinate all receptive stigmas within range of the trees of the variety shedding pollen.

The estimated dates of first and last pollen shedding and of the major pollen-shedding periods are given in table 2. There were wide

TABLE 2.—*Dates and duration of the periods of pollen shedding of several varieties of pecan during 3 seasons*

Variety	Dates of first and last observed pollen shedding	Major pollen-shedding period [1]		Total length of pollen-shedding period
		Dates	Length of period	
			Days	*Days*
DENISON, 1933				
Burkett	May 4–11	May 5–10	6	8
Schley	May 3–10	May 5–9	5	8
Stuart	May 5–12	May 6–11	6	8
Sovereign	Apr. 24–May 7	Apr. 25–May 3	9	14
Squirrel	Apr. 24–May 8	Apr. 25–May 5	11	15
Western	Apr. 25–May 8	Apr. 26–May 5	10	14
San Saba Improved	do	Apr. 27–May 5	9	14
Success	Apr. 26–May 10	Apr. 28–May 7	10	15
Clark	do	Apr. 28–May 8	11	15
AUSTIN, 1934				
Moneymaker	Apr. 29–May 12	May 1–7	7	14
Burkett	Apr. 30–May 12	May 2–9	8	13
Delmas	May 1–14	May 3–11	9	14
Schley	May 1–12	May 4–10	7	12
Kincaid	Apr. 30–May 12	May 3–11	9	13
Sovereign	Apr. 21–May 3	Apr. 23–May 1	9	13
ROGERS, 1935				
Jersey	Apr. 17–May 2	Apr. 18–27	10	16
Burkett	Apr. 18–May 5	Apr. 20–30	11	18
Delmas	Apr. 18–May 1	Apr. 21–30	10	14
Schley	Apr. 19–30	Apr. 21–28	8	12
Sovereign	Apr. 10–25	Apr. 12–22	11	16
San Saba Improved	Apr. 10–23	Apr. 11–22	12	14
Western	Apr. 13–May 2	Apr. 15–27	13	20
Success	Apr. 14–26	Apr. 15–22	8	13
Williamson	Apr. 14–24	do	8	11
Squirrel	Apr. 16–30	Apr. 16–25	10	15
Halbert	Apr. 12–May 2	Apr. 15–27	13	21
Clark	Apr. 12–May 7	Apr. 16–May 1	16	26
Onliwon	Apr. 11–May 2	Apr. 14–29	16	22

[1] Estimated dates and duration of period from the time 1 percent to the time 99 percent of pollen was shed. The major period includes first and last dates as given in column 3, since each date represents the preceding 24-hour period during which at least 1 percent of the pollen was shed.

differences in the lengths of the pollen-shedding periods of the different varieties in the same season as well as wide differences within the same variety in different seasons. For instance, the Burkett variety shed pollen over a period of 8 days in 1933, 13 days in 1934, and 18 days in 1935, while the major pollen-shedding periods for the same years were 6, 8, and 11 days, respectively. The Clark variety shed pollen over periods of 15 and 26 days, respectively, in 1933 and 1935, while the corresponding major periods were 11 and 16 days. The total length of the pollen-shedding periods varied from 8 days for the Burkett, Schley, and Stuart varieties in 1933 to 26 days for the Clark variety in 1935, while the major periods varied from 5 days for the Schley variety in 1933 to 16 days for the Clark variety in 1935. The three series of experiments were conducted in different years, in different localities, and with trees having different types of shoot growth. These factors probably were largely responsible for the variations in pollen-shedding periods of the same variety in the different years.

DICHOGAMY

Protandrous and Protogynous Varieties

The relationship of the major pollen-shedding period to the major receptive period of each variety is shown graphically in figure 4. In no instance are the two periods closely concurrent, and in several cases they do not overlap at all. The varieties fall into two groups with reference to the relative time at which pollen is shed as compared with the time the stigmas are receptive. In one group (protandrous) the pollen is shed early and in the other group (protogynous), it is shed late, as compared with stigma receptivity.

The staminate flowers of the protandrous varieties develop more rapidly than those of the protogynous varieties, but the pistillate flowers develop in the reverse order. As a general rule, pollen is shed earlier and stigma receptivity is later in protandrous varieties than in protogynous varieties (fig. 4). However, the time at which a variety matures its staminate and pistillate flowers in any season depends to a large extent upon the time of growth initiation in the spring. In extreme cases the pollen-shedding period of a protandrous variety may coincide with that of a protogynous variety if the protandrous variety starts growth late in the spring. Likewise the pollen-shedding period of an especially early protogynous variety may coincide with that of a protandrous variety or may be even earlier than some protandrous varieties.

Degree of Dichogamy in Different Varieties

During the course of these experiments it became apparent that the degree of dichogamy was not the same in all varieties. Experiments to determine this point more definitely were carried out in 1935. In the case of protogynous varieties, pistillate clusters were bagged before the stigmas were receptive. Later some of these clusters were pollinated when observations indicated that a high percentage of the stigmas were receptive; the others were not pollinated until just at the time pollen was being shed by the catkins on the same twigs that bore the pistillate clusters. It was assumed that varieties setting a relatively high percentage of the nuts pollinated at that time could be considered

self-fruitful during that year. The data obtained (table 3) show that in only one variety was the set of nuts as high from pollinations made at the time of pollen shedding as from earlier pollinations. In several of the varieties dichogamy was complete, no nuts being set when pollinations were delayed until the pollen had begun to shed; in other varieties the degree of dichogamy varied greatly. In the Russell, Odom, Kincaid, Delmas, and Schley varieties the degree of dichogamy was less than in the others used.

TABLE 3.—*Relative degree of dichogamy in several pecan varieties in the protogynous group, season of 1935*

Variety	Pollinated before pollen shed by catkins on same branch [1]				Pollinated at start of pollen shedding on same branch [1]			
	Period of pollination	Nuts used	Nuts set		Period of pollination	Nuts used	Nuts set	
		Number	*Number*	*Percent*		*Number*	*Number*	*Percent*
Humble	Apr. 12	83	24	28.9	Apr. 20–24	92	0	0.0
Bowers	do	59	2	3.4	Apr. 21–25	66	0	.0
Elgin	do	39	12	30.8	Apr. 22–25	66	0	.0
Russell	Apr. 18	17	7	41.2	Apr. 22–24	23	9	39.1
Odom	Apr. 16–20	31	14	45.2	do	23	5	21.7
Kincaid	Apr. 18	63	16	25.4	Apr. 23–27	93	25	26.9
James	do	85	33	38.8	Apr. 24–27	121	1	.8
Teche	do	76	20	26.3	do	78	0	.0
Alexander	Apr. 20	37	24	64.9	do	44	8	18.2
Mosty	Apr. 18	19	17	89.5	Apr. 23–29	74	12	16.2
Mahan	Apr. 16–20	146	60	41.1	Apr. 24–28	112	5	4.5
Stuart	Apr. 25	58	22	37.9	Apr. 24–May 1	83	4	4.8
Curtis	Apr. 27	44	26	59.1	Apr. 29–May 6	44	2	4.5
Jersey	Apr. 10–12	184	81	44.0	Apr. 17–23	48	0	.0
Burkett	Apr. 14–16	74	27	36.5	Apr. 18–25	60	0	.0
Delmas	Apr. 16–18	125	37	29.6	Apr. 19–24	37	8	21.6
Schley	do	96	28	29.2	Apr. 22–24	39	7	17.9

[1] The branch referred to is the twig of the previous season's growth from which grew the current shoots bearing pistillate clusters.

In the protandrous varieties, shoots were tagged at the time pollen shedding began and the time interval between this date and that when the first stigmas on these branches were receptive was determined. Stigma receptivity was found by pollinating and then bagging different pistillate clusters at varying intervals after the beginning of pollen shedding, and later counting the number of nuts set. The data obtained were insufficient to warrant conclusions, but, together with the data secured in the receptivity experiments, they indicate that the degree of dichogamy in this group varies as much as in the protogynous varieties. The degree of dichogamy of a variety may vary from season to season, but in no case was it found to vary enough to shift the type of dichogamy from protandrous to protogynous, or vice versa.

DISCUSSION

The graphs representing the set of nuts from day-to-day pollinations show considerable fluctuation (figs. 2 and 3). These fluctuations are ascribed chiefly to nonuniformity in the samples, to loss of nuts from insect damage, and to other conditions, not associated with the lack of pollination or fertilization, that prevailed generally after the bags were removed and before the set of nuts could be recorded. In general, the receptivity curves of all varieties were of the same form, showing a relatively high set of nuts over a considerable time within the recep-

tive period and indicating a relatively long period of receptivity of individual stigmas. Since the percentage of clusters set varied approximately with the percentage of nuts set, it is also indicated that all stigmas in a cluster became receptive within a very short time. Further experiments are being conducted to determine more definitely the length of the receptive periods of individual stigmas and the variation in time at which the individual stigmas in a cluster become receptive.

There was considerable variation in the total length of the period of stigma receptivity of a given variety in different years and also a difference in the total length of the periods of stigma receptivity of different trees in the same year. The differences occurring in the same year are attributed largely to variations in growth and development of the shoots bearing the pistillate clusters, and the differences occurring in different years may be influenced by these factors and by seasonal variations. The extent to which the development of the shoots sometimes varied from the average is shown in figure 6. It was observed also that buds starting growth early were early in maturing flowers, and vice versa. Therefore, the lack of uniformity in the development of the stigmas probably was due largely to the difference in time at which the buds producing pistillate shoots started growth. The interval between the time of initiation of growth of the earliest and latest buds on a tree varied somewhat according to the way the tree had grown the previous season. The shoots on slow-growing trees were more uniform in initiation of growth and flower development than those on fast-growing trees. Therefore, the total length of the receptive period of the stigmas varied with different trees of a variety, and when there was a difference of several days in the time of general growth initiation in the trees the receptive period was longer. This variation might also affect the length of major periods of stigma receptivity, but these were usually affected less than the total receptive periods. The same relationship held in the development of the staminate flowers and the shedding of pollen.

It was observed that a period of rain or fog halted the opening of the anthers, but apparently the high humidity affected only the mechanism of anther dehiscence and not the pollen-ripening processes, since such periods were generally followed by unusually heavy pollen shedding. During the 3 years of the experiment there were never 2 consecutive days during which no pollen was shed on account of rain or high humidity.

The degree of dichogamy varied widely but was high in most of the varieties used in these experiments. Therefore, in planting a pecan orchard or in top-working a seedling grove provision should be made to insure adequate pollination by the use of two or more varieties selected so that pollen will be shed during the major receptive periods of all the varieties used. In general, a good crop of nuts is possible if 50 percent or more of the stigmas on the trees set nuts, and at least 50 percent of the stigmas should be pollinated if the major periods of receptivity and pollen shedding overlap by 1 or more days when conditions are favorable for pollen shedding. However, it is desirable that pollen be shed throughout the major periods of receptivity of all varieties, and this condition is attained by selection and interplanting of the proper protogynous and protandrous varieties. It is noted

from the data (fig. 4) that in general the protogynous varieties shed pollen at a time when a high percentage of the stigmas of the protandrous varieties were receptive, and vice versa. However, this may not always occur, because it is possible for the pollen-shedding periods of some protogynous varieties to coincide with those of some protandrous varieties, as previously pointed out. In such a case neither variety would furnish adequate pollen for the other, because the receptive period of the stigmas of the protogynous variety would be almost past before pollen shedding began and receptivity of the stigmas of the protandrous variety would be just beginning at the time pollen shedding was completed.

If climatic variations in the spring cause a change in the interval between the staminate and pistillate flowering periods that is favorable to protogyny or protandry, it is assumed that all varieties will be shifted in the same direction, though possibly not to the same degree. If this is true, the interval between the pistillate and staminate flowering periods should be increased in protandrous varieties in a season favoring protandry but decreased in protogynous varieties in such a season. Similarly the interval should be decreased in protandrous varieties in a season favoring protogyny but increased in protogynous varieties under the same conditions. A study of the data, which are not entirely consistent, indicates neither a pronounced nor a uniform shift toward either protandry or protogyny in any variety during the 3 years.

SUMMARY

The receptive periods of the stigmas of 16 varieties of the pecan were determined during one to three seasons. There was a wide variation in the length of the periods of stigma receptivity of different varieties in the same year and of the same variety in different years. The variations in the same variety may be ascribed to variation in time of initiation of growth of buds producing pistillate shoots and to seasonal variations.

Studies made on 12 varieties showed that all unpollinated nuts dropped within a period of 5½ to 6½ weeks after the last date of stigma receptivity.

The range in maturity of staminate flowers varied in the same way as the pistillate flowers, but pollen shedding was irregular owing to changes in weather conditions.

Pecan varieties may be placed in two groups according to blossoming characteristics. In one group, pollen shedding occurs relatively early and stigma receptivity relatively late; in the other, the relative time of maturity of the flowers is reversed. However, the actual time at which the flowers of one tree mature as compared with those of other trees is also dependent on the time of growth initiation and the relative rate of shoot growth and flower development.

The degree of dichogamy of different varieties was found to vary widely. In some instances sufficient coordination existed for a good set of nuts by self-pollination, whereas in other cases only a very little or no self-pollination was evident.

No case of a pronounced shift in dichogamy, either toward protandry or protogyny, was found in any variety during the three seasons of the experiment.

INEFFECTIVENESS OF PROPRIETARY REMEDIES AND OTHER DRUGS IN THE CONTROL OF BANG'S DISEASE, WITH SPECIAL REFERENCE TO "3-V TONIC" AND "BOWMAN'S" [1]

By A. B. CRAWFORD, *senior veterinarian, Animal Disease Station, Bureau of Animal Industry, United States Department of Agriculture,* and B. A. BEACH, *professor of veterinary science, Wisconsin Agricultural Experiment Station*

USE OF THERAPEUTIC AGENTS IN BANG'S DISEASE

In the investigation of Bang's disease by Federal and State experiment stations and some privately operated laboratories, much effort has been spent in studying the effect of various drugs on this disease. It was hoped to find some agent which could penetrate the tissues of the affected animal in sufficient concentration to destroy the *Brucella abortus* germs causing the disease without damage to the tissues themselves. A large number of different chemical substances which have recognized therapeutic value have been tried by various experiment stations and laboratories, but not one of these products has been proved, in controlled experiments, to have any value in the prevention or cure of Bang's disease. Recently, sulfanilamide, a chemical product which has been found to be very effective in the treatment of certain streptococcic infections and which has been reported to be of some benefit in the treatment of brucellosis in man, was tried in cattle affected with Bang's disease. Although the quantity fed was only slightly less than the toxic dosage, it had no apparent action in destroying the *Brucella* organisms or reducing their number or virulence.

Thus the history of drugs or other therapeutic chemicals in the treatment of Bang's disease has been negative so far as finding any substance which has a specific action on *Brucella* organisms in the tissues of animals. These results have been published from time to time in veterinary literature, but in spite of this fact so-called remedies for Bang's disease still appear on the market. Many thousands of dollars have been spent by farmers for such worthless products.

CONTROL OF CONCERNS PRODUCING BANG'S DISEASE REMEDIES

Remedies for Bang's disease, commonly called abortion cures, are subject to control under the Federal Food and Drug Act. Although the United States Food and Drug Administration has been active in the enforcement of that law as it relates to such products, the statute does not cover advertising as such or products marketed within the State in which they are produced. Protection against false advertising of such products is afforded, however, under the Wheeler-Lea Amendments enforced by the Federal Trade Commission.

Undoubtedly the most important factor in the sales promotion of Bang's disease remedies is literature containing testimonials from

[1] Received for publication April 26, 1939.

livestock owners who have used such products in their infected herds. The sincerity of the writers of these testimonials is not questioned by investigators who have studied the nature of Bang's disease, but these investigators know that any apparent improvement in an affected herd following the use of the "cure" was not due to medication, but was a natural sequence in the course of the disease.

NATURE OF BANG'S DISEASE

When Bang's disease first appears in a herd, it is followed by a wave of abortions in the pregnant animals. This period lasts for 1 or 2 years, or until all susceptible pregnant animals have contracted the disease. This, known as the active stage of the disease, is followed by the chronic stage. When cows have contracted the disease and aborted, many will still harbor the *Brucella* organisms, but in spite of this fact—and this point is to be especially noted—they rarely abort at subsequent pregnancies. This ability of the animals to carry full-term calves in spite of being infected is due to immunological changes which have developed within their bodies. During the active stage of Bang's disease, 15 to 50 percent of the pregnant animals will abort. In some herds the percentage is much higher. When the disease has reached the chronic stage, however, there may be no abortions or only a small percentage, most of which are confined to replacements in the herd or heifers subjected to exposure for the first time. An owner does not use a "cure" if his herd is free from the disease. Generally before it is used, the disease will be approaching the end of the active stage. Thus after using the cure, the owner will note that the abortions have greatly decreased or practically ceased, and it is only natural that he should assume that the remedy was responsible for the apparent improvement of the herd. However, his herd is still infected and will remain so until the animals carrying the infection are removed.

PURPOSE OF TESTS OF SO-CALLED CURES

Federal and State investigators of Bang's disease and State livestock sanitary officials have long known that hundreds of farmers and herd owners have been and still are paying out their hard-earned money for the purchase of so-called remedies which are worthless in the prevention or cure of this disease. Authorities are powerless, however, to stop such sales in the absence of direct violation of Federal or State law. To prevent further losses to owners of infected herds through the purchase of such products, the Congress of the United States passed an amendment to the Agricultural Administration Act permitting a portion of the funds appropriated under this act to be spent in testing various proprietary remedies alleged to be preventives or cures for Bang's disease.

Obviously, it was impracticable to submit all alleged remedies for Bang's disease to controlled tests with the money made available. Therefore, two products which were believed to be the most widely advertised and used were selected for test. These products were (1) 3–V Tonic, manufactured by the Crawford Co., Winona, Minn., and (2) Bowman's, manufactured by the Bowman Laboratory, Owatonna, Minn.

These tests [2] were made in the State of Wisconsin in 1936 and 1937. Professional employees of both the Bureau of Animal Industry and the University of Wisconsin participated in their planning and performance.

A description of the testing of each of these products, covering the history and treatment of each animal, a chemical analysis of the respective products, and a summary of results, is given in the following pages.

CRAWFORD 3–V TONIC

The 3–V Tonic was obtained from T. E. Crawford, of the Crawford Co. An analysis of the product made by the United States Food and Drug Administration showed it to consist essentially of lime, basic magnesium carbonate, charcoal, a soluble compound of sulfur and calcium, probably calcium hyposulfite, small proportions of ferrous sulfate, sulfur, and powdered linseed, and a smaller proportion of powdered ginger.

It was claimed for the 3–V Tonic that it would prevent abortion and enable cattle affected with Bang's disease to bear normal, healthy, full-term calves. To determine whether the claims made were based on facts, and also whether the product would prevent or cure Bang's disease, the following experiment was made.

EXPERIMENTAL PROCEDURE

Sixty heifers that were believed to be pregnant were purchased from herds with a negative history of abortions. These herds had previously been subjected to from one to five Bang's disease tests, and no evidence of infection had been found. The heifers gave negative results to the Bang's disease test at the time they were obtained. They were placed on a farm that had been rented for the experimental work. It was located a few miles from the University of Wisconsin. The heifers were examined for pregnancy before they were purchased. They were divided into three groups similar as to condition but were kept in the same barn and allowed to mingle in an exercising yard.

To determine its preventive effects, the 3–V Tonic was fed to 20 heifers in group 1 before they were exposed to *Brucella abortus*. To determine the curative effects, group 2, likewise consisting of 20 heifers, was fed the product after exposure to *Br. abortus*. Group 3 received none of the product but served as controls on the other two groups.

Beginning with the evening feeding on October 12, 1936, the product, mixed with the morning and evening feed, was fed regularly to group 1 in accordance with directions prescribed by the manufacturer. Each animal received one-half ounce (1 tablespoonful) of the material daily for 75 days. The total quantity fed to each animal during the entire period was 2⅛ pounds.

[2] The tests were planned and directed by W. E. Cotton, superintendent, and J. M. Buck, assistant superintendent, of the Animal Disease Station, Bureau of Animal Industry, with the cooperation of E. G. Hastings, B. A. Beach, and Noble Clark, of the Wisconsin Agricultural Experiment Station. Following the retirement of Dr. Cotton, September 30, 1937, Dr. Buck assembled the data for this report. After the death of Dr. Buck on May 2, 1938, A. B. Crawford, of the Animal Disease Station, completed the report, which was reviewed and approved, with slight revision, by the representatives of the Wisconsin Agricultural Experiment Station. (There is no relation between A. B. Crawford, the senior author of this paper, and T. E. Crawford, of the Crawford Co., the producer of 3–V Tonic, the similarity of names being coincidental.) J. S. Healy, of the U. S. Bureau of Animal Industry, Madison, Wis., supervised the feeding and management of the experimental herds.

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Feeding of the product to group 2 was begun with the evening feeding of November 28, 1936, the day the animals were subjected to *Br. abortus* exposure, and continued for 75 days, the animals in this group receiving the same doses and in the same manner as those in group 1.

On November 28, 1936, when the heifers in group 1 had been fed the product for 48 days, all the animals in the three groups, with the consent of T. E. Crawford, were exposed to *Brucella abortus*. The feeding of the product to the animals in group 1 was then continued for 27 days in order to complete a 75-day feeding period.

The exposure of the cattle to *Brucella abortus* was made by representatives of the United States Bureau of Animal Industry and the University of Wisconsin in the presence of T. E. Crawford, who, after it had been completed, expressed himself as considering it very fairly carried out.

The method of exposing the heifers to Bang's disease was through the mucus membrane of the eye. A suspension of *Brucella abortus* (bovine) was prepared with three strains of the micro-organism, designated, respectively, 213, 1927, and 214. Strain 213 had been isolated, about 1 year previously, from the lymph glands associated with the udder of an infected cow; strain 1927 had been recently isolated from an aborted fetus; and strain 214 had been recently isolated from the milk of an infected cow. Three small drops of the suspension were instilled in the mucous membrane of one eye of each animal. In no instance was any of the suspension seen to escape from the eye cavity. Use was made of but 8 cc. of the suspension to expose the 60 heifers, each heifer receiving 0.13 cc. of the material. This method of exposure to Bang's disease has been extensively used in vaccination experiments conducted by the United States Bureau of Animal Industry because it provides a dependable way of transmitting the disease to pregnant cattle that possess normal resistance to it.

All the heifers gave negative results to the agglutination test for Bang's disease on December 4, 1936, 6 days after they were exposed. On the next test, which was made 13 days after they received eye exposure, all 60 animals reacted to the test in titers ranging from 1 to 50 to 1 to 400. Their reactions, in nearly all cases, gradually increased in intensity until a titer of 1 to 6,400 or higher was reached.

When the gestation period of each heifer terminated, several guinea pigs were injected with a sample of her uterine material and others with a composite sample of her colostrum to determine whether *Brucella abortus* was present in these substances. In the event that the heifer aborted, the fetus was cultured.

RESULTS OF THE EXPERIMENT

One of the heifers in group 1, treated with the product before exposure, had to be eliminated from the experiment because of accident and one control proved to be nonpregnant. There were, therefore, 58 heifers which completed the experiment and for which results are available. These are shown in table 1. Fifty-two of the animals aborted, and 6 gave birth to weak calves with insufficient vigor to survive. *Brucella abortus* was isolated from all but 6 of the fetuses—3 of the controls and 3 of the group that was fed the product after

TABLE 1.—*Results of feeding Crawford 3–V Tonic to pregnant heifers to prevent or cure Bang's disease*

[Date of *Brucella abortus* eye exposure in the 3 groups, Nov. 28, 1936; in group 1, date of first feeding, Oct. 12, and date of last feeding, Dec. 25, 1936; in group 2, date of first feeding, Nov. 28, 1936, and date of last feeding, Feb. 11, 1937]

GROUP 1.—FED PRODUCT 48 DAYS PRIOR TO AND 27 DAYS SUBSEQUENT TO EXPOSURE

Animal designation	Date of termination of gestation	Outcome of pregnancy	Approximate stage of pregnancy	Results of examination for *Brucella abortus*[1]	
				Uterus	Colostrum
	1936		*Months*		
DJ 14304	Dec. 27	Abortion	6	+	+
	1937				
DK 64423	Jan. 2	do	7½	+	+
DH 74369	Jan. 4	do	6½	+	+
DH 65869	Jan. 5	do	8½	+	+
DE 54524	Jan. 11	do	6	+	+
DK 74136	Jan. 13	do	6	+	o
DS 87971	Jan. 14	do	5½	+	+
DA 75155	do	do	7½	+	+
DH 62400	do	do	7	+	o
DH 80354	Jan. 15	do	7½	+	+
DH 80363	Jan. 18	do	8	+	o
DE 15741	do	do	7	+	+
DJ 65870	Jan. 20	do	6½	+	o
DJ 14305	Jan. 26	do	7	+	+
DS 87969	Jan. 27	do	6	+	+
DK 64363	Feb. 1	do	6½	+	+
DK 64888	Feb. 4	do	6½	+	o
DH 46564	do	do	7	+	o
DS 33355	Feb. 7	do	6½	+	+
GROUP 2.—FED PRODUCT SUBSEQUENT TO EXPOSURE ONLY					
	1936				
DS 45047	Dec. 27	Abortion	6½	+	+
DJ 60305	Dec. 29	do	6	+	+
	1937				
DB 57572	Jan. 1	do	6½	+	+
DH 46913	Jan. 3	do	6½	+	+
DS 45043	Jan. 4	do	7	+	+
DS 45046	Jan. 7	do	7	+	+
DS 38714	Jan. 14	do	7	+	+
DS 44824	Jan. 18	do	7	+	o
DH 80340	Jan. 19	Weak calf (died)	7	−	+
DS 15129	Jan. 23	Abortion	7	+	+
DH 80342	Jan. 23	do	7½	+	+
DJ 30446	Jan. 24	Weak calf (died)	7½	+	+
DA 55134	Jan. 27	Abortion	7	+	+
DS 94161	Feb. 1	do	7½	+	+
DA 75159	Feb. 2	Weak calf (died)	8	+	+
DS 87944	Feb. 3	do	7	+	+
DA 55713	Feb. 4	Abortion	7	+	o
DH 30449	Feb. 8	do	8	+	+
DK 64886	Feb. 24	do	8	−	+
DH 30422	Mar. 6	do	7½	+	+
GROUP 3.—CONTROLS (NOT FED PRODUCT)					
	1937				
DK 74131	Jan. 8	Abortion	6	+	+
DK 74133	Jan. 8	do	5	+	+
DS 45048	Jan. 12	do	7	+	+
DS 87973	Jan. 13	do	5	+	+
DJ 24128	Jan. 15	do	7½	+	+
DH 80367	Jan. 17	do	8	+	+
DS 910	Jan. 18	do	6	+	+
DS 94162	Jan. 20	do	6	+	+
DH 80344	Jan. 23	do	7½	+	+
DJ 30420	Jan. 24	Weak calf (died)	7½	+	+
DJ 30421	Jan. 25	Abortion	7½	+	+
DS 72367	Feb. 4	do	6	+	o
DH 46912	Feb. 16	Weak calf (died)	8	+	+
DA 55724	do	Abortion	7½	−	+
DJ 43492	Feb. 20	do	6	+	+
DJ 43491	Feb. 23	do	6½	+	+
DK 64887	Feb. 27	do	7	−	+
DH 80348	Mar. 5	do	6½	+	+
DH 76369	Mar. 6	do	7	+	+

[1] +, *Br. abortus* present; −, *Br. abortus* absent; o, not determined.

exposure only. However, the infection was present in uterine materials or colostrum, and in most cases in both of these substances, of all 58 cattle when their gestations terminated.

The first abortion occurred December 27, 1936, 29 days after the heifer was exposed to *Brucella abortus*. Abortions continued to occur until the early part of March 1937.

Of the 19 heifers in group 1, which was fed the product 48 days prior to and 27 days subsequent to exposure, all aborted. Of the 20 heifers in group 2, which received the product subsequent to exposure only, 16 aborted and 4 gave birth to weak calves that did not survive. Of the 19 control heifers in group 3, which did not receive the product, 17 aborted and 2 gave birth to weak calves that did not survive.

The results of this carefully controlled test indicate that the Crawford 3–V Tonic was ineffective in preventing pregnant heifers from becoming infected with Bang's disease or in preventing them from aborting after having acquired it.

BOWMAN'S PRODUCT

An analysis of the Bowman's product by the United States Food and Drug Administration showed it to be a light-brown granular material containing sugar (sucrose), 90.3 percent; invert sugar, 4.3 percent; wood creosote, 0.1 percent; ash, 1.5 percent; and moisture by difference. No other ingredients were detected.

In order to obtain definite information as to whether this product possesses value as a preventive or cure for Bang's disease or in causing the disappearance of *Brucella abortus* agglutinins from the blood serum of cattle which have acquired it, the following experiment was made.

EXPERIMENTAL PROCEDURE

Forty heifers were purchased from farms that were free from Bang's disease. As a result of pregnancy examinations, all the heifers were believed to be from 6 weeks to 4 months with calf. They gave negative results to the agglutination test for Bang's disease at the time they were purchased as well as after their delivery at the farm where the test was carried on. This farm was located a few miles from the University of Wisconsin and had been rented for making the test. Here the animals were divided into 2 groups of 20 each, similar as to condition. The Bowman's product was fed to the heifers in group 1 in accordance with the directions of the manufacturer. The heifers in group 2 were employed as controls, receiving none of the product. The Bowman's product fed to the experimental cattle was obtained indirectly by purchase in the original sealed packages, as the manufacturer of it was unwilling to cooperate in a test of the sort outlined and performed.

The 20 heifers in group 1 received four series of feedings of the product, consisting of four doses of 2 pounds each in accordance with the directions appearing on the labels of the packages. It was mixed with a small quantity of millfeed and given to the heifers in the morning before their regular feeding was commenced. It was consumed promptly by them.

The first series of feedings was on March 24, 25, 27, and 29, 1937. The feeding of the product was then discontinued for 1 week, when

the second series of feedings was commenced. These four feedings were administered on April 6, 8, 10, and 12. Feeding was again discontinued for a little more than 2 months, and the third series of feedings was given on June 19, 21, 23, and 25. After an interval of 30 days, the fourth series of feedings was given on July 23, 25, 27, and 29. Each heifer in group 1 thus received, during the four series of feedings, 16 doses of the product consisting of 2 pounds each, a total quantity of 32 pounds.

The 40 heifers in groups 1 and 2 were exposured to Bang's disease April 14, 1937, 2 days after the heifers in group 1 had received the second series of feedings. The *Brucella abortus* exposure of the cattle was made by representatives of the United States Bureau of Animal Industry and the University of Wisconsin. Use was made of the conjunctival method, which consisted in instilling a very small quantity of a suspension of *Br. abortus* in the mucous membrane of the eye. The suspension of *Br. abortus* used was prepared with three strains of the micro-organism, designated respectively, 213, 1927, and 214. Strain 213 had been isolated from the supramammary lymph glands of an infected cow about 14 months previously; strain 1927 had been isolated from an aborted fetus about 6 months previously; and strain 214 had been obtained about 6 months before from the milk of an infected cow. Three small drops of the suspension were deposited on the mucous membrane of one eye of each animal. Use was made of but 5 cc. of the suspension to expose the 40 heifers, each animal thus receiving 0.12 cc. of the material.

All the heifers gave negative results to the Bang's disease agglutination test on April 14, 1937, the day they were subjected to *Brucella abortus* exposure. On the next test, which was made April 20, 6 days later, one of the treated heifers and one of the controls gave a suspicious reaction to the test. The remaining heifers gave negative results. On the third test, which was made April 26, 12 days subsequent to their exposure, all the heifers reacted to the agglutination test in titers of from 1 to 50 to 1 to 400, there being but a slight difference between the intensity of the reactions of the treated heifers and the controls. The titers of the reactions given by the heifers in both groups gradually increased until they became 1 to 3,200 or higher.

When the gestation period of each heifer terminated, two guinea pigs were injected with a sample of her uterine material and four others with a composite sample of her colostrum for the purpose of determining whether *Brucella abortus* was present in these substances. In the event the heifer aborted, the fetus was cultured.

RESULTS OF THE EXPERIMENT

The results of the experiment (table 2) were obtained on 19 heifers that were fed the Bowman's product and 20 controls that did not receive it. One heifer that received the product was eliminated from the experiment before its completion because she was found to be nonpregnant.

The first abortion occurred May 12, 1937, 28 days subsequent to *Brucella abortus* exposure. The last of the 39 heifers completed her gestation period December 27, 1937.

Of the 19 heifers in group 1 which received eight doses of the Bowman's product previous to *Brucella abortus* exposure and eight doses

subsequent to exposure, 1 produced a vigorous calf, 1 a weak calf which lived, and 1 a weak calf which died. Sixteen heifers aborted. *Br. abortus* was demonstrated to be present in the uteri or colostrum, or both, of the 19 heifers when their pregnancies terminated and was isolated from the fetuses of 11 of the 16 heifers which aborted.

Of the 20 controls in group 2 which did not receive the product, 1 produced a vigorous calf and 4 others produced weak calves which died. Fifteen of the heifers in this group aborted. The presence of *Brucella abortus* was demonstrated in the uterine material or colostrum, or both, of all 20 heifers. The organism was isolated from the fetuses of 12 of the 15 heifers which aborted.

TABLE 2.—*Results of feeding Bowman's product to pregnant heifers to prevent or cure Bang's disease*

[In both groups, date of *Brucella abortus* exposure, Apr. 14, 1937. In group 1, date of first feeding, Mar. 24, and date of last feeding, July 29, 1937; number of feedings, 16]

GROUP 1.—ANIMALS FED PRODUCT

Animal designation	Date of termination of gestation	Outcome of pregnancy	Approximate stage of pregnancy	Results of examination for *Brucella abortus*[1]	
				Uterus	Colostrum
	1937		*Months*		
DS 76550	May 21	Abortion	6	+	+
DX 9903	May 25	do	4	+	+
EA 79101	May 28	do	4	−	+
DS 4806	June 6	do	3	+	+
DS 4923	June 7	do	4	+	+
DS 4924	June 20	do	3½	+	−
DS 76818	July 1	do	4	+	+
DX 9901	do	do	4	+	−
DS 76817	July 5	do	4	+	+
DS 4930	July 8	do	3½	+	+
DS 4926	July 12	Weak calf (lived)	4½	+	+
DS 4808	July 13	Abortion	4½	+	+
DS 4925	July 14	Weak calf (died)	5½	+	+
DS 4807	July 16	Abortion	4½	+	+
DS 4804	July 21	do	3½	+	+
DX 9947	July 26	do	4	+	+
DS 76554	July 27	do	3	+	+
DX 9918	Sept. 17	Vigorous calf	4	−	+
DS 4928	Aug. 26	Abortion	4½	+	+

GROUP 2.—CONTROLS (NOT FED PRODUCT)

	1937				
EA 67391	May 12	Abortion	5½	+	+
DH 95809	May 23	do	4	+	+
DH 80416	May 26	do	4½	+	+
EA 7914	May 29	do	4½	+	−
DB 99858	do	do	4	+	+
DJ 19847	May 31	do	4½	+	+
DS 42803	do	do	4	+	+
EA 31533	June 6	do	4	+	−
EA 67395	June 14	Weak calf (died)	5½	+	+
EA 31522	June 19	Abortion	4½	+	+
DJ 19848	June 28	Weak calf (died)	5	+	+
DJ 81035	July 1	Abortion	4	+	−
EA 31525	July 4	do	3½	+	+
EA 67392	July 20	do	3½	+	+
DX 9923	July 21	do	3½	+	+
EA 31524	Aug. 3	do	2½	+	+
DH 95810	Aug. 19	do	3½	+	+
DH 80417	Sept. 13	Weak calf (died)	3½	−	+
DH 80419	Aug. 19	Vigorous calf	3½	+	−
EA 31529	Dec. 27	Weak calf (died)	3	0	+

[1] +, *Br. abortus* present; −, *Br. abortus* absent; 0, not determined.

The results of the experiment, therefore, definitely show that the Bowman's product was ineffective either in the prevention or cure of Bang's disease. Each heifer in group 1 received eight 2-pound doses of the product before exposure to *Brucella abortus* and the same quantities after exposure. However, the animals exhibited no more resistance to the disease than the heifers in group 2 that did not receive the product.

INEFFECTIVENESS OF PRODUCT IN CAUSING DISAPPEARANCE OF BRUCELLA ABORTUS AGGLUTININS FROM BLOOD OF CATTLE

To determine whether the Bowman's product is effective in causing the disappearance of *Brucella abortus* agglutinins from the blood serum of cattle reacting to the agglutination test for the disease, 10 of the heifers in group 1 and 10 of those in group 2 were retained for several months after their pregnancies had terminated and agglutination tests made of their blood serum at about monthly intervals. The results are shown in table 3.

TABLE 3.—*Results of tests to determine the effectiveness of Bowman's product in reducing Brucella abortus agglutinins in the blood serum of cattle reacting to the agglutination test for Bang's disease*

Group No.[1]	Blood titer on indicated number of days after exposure							
	70		98		119		148	
	Average	Minimum	Average	Minimum	Average	Minimum	Average	Minimum
1 (fed Bowman's)	1:2,510	1:800	1:4,080	1:800	1:6,560	1:400	1:23,200	1:3,200
2 (not fed Bowman's)	1:2,250	1:800	1:2,920	1:800	1:4,560	1:400	1:27,680	1:800

Group No.	Blood titer on indicated number of days after exposure					
	181		202		238	
	Average	Minimum	Average	Minimum	Average	Minimum
1 (fed Bowman's)	1:24,000	1:400	1:18,080	1:400	1:23,520	1:400
2 (not fed Bowman's)	1:18,440	1:400	1:10,280	1:400	1:14,290	1:400

[1] 10 animals in each group.

The Bowman's product was found to be ineffective in causing catttle reacting to the Bang's disease agglutination test to become nonreactors to the test or in otherwise having any demonstrable effect on the *Brucella abortus* agglutinin concentration in the blood serum of cattle affected with the disease. As shown by table 3, about 8 months after the two groups of animals were infected with the disease, the average agglutination titer of the blood serum of the group which had received 32 pounds of Bowman's product was higher than that of the group which had not received it.

SUMMARY AND CONCLUSIONS

In work on Bang's disease and possible methods for its control, Federal and State experiment stations have studied the effect of various drugs and chemical substances. In every instance the drug or chemical tested has given negative results, but in spite of these findings and the wide publicity given them, so-called remedies for Bang's disease still appear on the market, and farmers continue to spend large sums for them.

The present study, conducted under Congressional authority, consisted of carefully controlled tests of two widely used, alleged remedies for Bang's disease, "3-V Tonic" and "Bowman's."

In the testing of 3-V Tonic, a group of 19 pregnant heifers, negative to the agglutination test, was fed this preparation prior to exposure to virulent strains of *Brucella abortus;* a second group of 20 heifers was fed prior and subsequent to exposure; and a third group of 19 heifers, as controls, received only exposure. All heifers in group 1 aborted; 16 heifers in group 2 aborted and 4 gave birth to weak calves; 17 heifers in the control group aborted and 2 gave birth to weak calves. *Brucella abortus* was recovered from uterine material or colostrum, and in most cases from both of these substances, in all 58 animals following parturition.

In the testing of Bowman's product, a group of 19 pregnant heifers, negative to the agglutination test, was fed this preparation prior and subsequent to exposure to virulent strains of *Brucella abortus;* a second group of 20 heifers, as controls, received only exposure. Of the 19 heifers in group 1, 16 aborted, 1 produced a weak calf which died, 1 a weak calf which survived, and 1 a vigorous calf. Of the 20 control animals, 15 aborted, 4 each produced a weak calf which died, and 1 a vigorous calf. *Brucella abortus* was recovered from uterine material or colostrum, or both, in each of the 39 heifers following parturition. Continued testing of the blood titer of 10 heifers in group 1 and 10 heifers in group 2, for a period of 8 months after exposure, showed that the feeding of Bowman's had no effect on reducing the blood titer following infection.

The 3-V Tonic and Bowman's product were thus found to be ineffective in preventing or curing Bang's disease. These results, together with previous negative findings obtained from other drugs and chemical substances, indicate that, in the light of present scientific knowledge, such products do not provide protection against the disease.

U. S. GOVERNMENT PRINTING OFFICE: 1940